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Bridging the gap between marine biogeochemical and fisheries sciences; configuring the zooplankton link

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Abstract

Exploring climate and anthropogenic impacts to marine ecosystems requires an understanding of how trophic components interact. However, integrative end-to-end ecosystem studies (experimental and/or modelling) are rare. Experimental investigations often concentrate on a particular group or individual species within a trophic level, while tropho-dynamic field studies typically employ either a bottom-up approach concentrating on the phytoplankton community or a top-down approach concentrating on the fish community. Likewise the emphasis within modelling studies is usually placed upon phytoplankton-dominated biogeochemistry or on aspects of fisheries regulation. In consequence the roles of zooplankton communities (protists and metazoans) linking phytoplankton and fish communities are typically under-represented if not (especially in fisheries models) ignored. Where represented in eco-system models, zooplankton are usually incorporated in an extremely simplistic fashion, using empirical descriptions merging various interacting physiological functions governing zooplankton growth and development, and thence ignoring physiological feedback mechanisms. Here we demonstrate, within a modelled plankton food-web system, how trophic dynamics are sensitive to small changes in parameter values describing zooplankton vital rates and thus the importance of using appropriate zooplankton descriptors. Through a comprehensive review, we reveal the mismatch between empirical understanding and modelling activities identifying important issues that warrant further experimental and modelling

investigation. These include: food selectivity, kinetics of prey consumption and interactions with assimilation and growth, form of voided material, mortality rates at different age-stages relative to prior nutrient history. In particular there is a need for dynamic data series in which predator and prey of known nutrient history are studied interacting under varied pH and temperature regimes.

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1. Introduction: changing perspectives of zooplankton in marine ecosystems

Prior to the 1980's, the structure of the ecosystem in the pelagic marine waters was typically described through what is now termed the "classical" food web (Steele, 1974; Cushing, 1975). Within this structure, primary production is attributed to photoautotrophic phytoplankton. These phytoplankton are then consumed by the "herbivorous" zooplankton (i.e., primary consumers) which are in turn ingested by carnivorous zooplankton and pelagic fish, which then serve as food for larger fish. Despite some earlier suggestions to modify this classic food web structure (e.g., Pomeroy, 1974), it was not until the early 1980's that the importance of microbial production gained recognition (Williams, 1981; Fenchel 1982), and the planktonic food web concept was broadened towards a more integrated view (the microbial food web). In this new defined structure phytoplankton as well as bacteria are consumed by protozoan grazers (Sherr and Sherr, 1994; Calbet, 2008), thus providing an additional food source for copepods and higher trophic levels. Following such studies, Azam et al. (1983) proposed the "microbial loop" as an addition to the food web, within which the dissolved organic carbon (DOC) is reincorporated into the food web mediated by prokaryotic activity.

The recognition of the importance of the microbial loop led to the link-sink debate (Gifford, 1991), questioning whether the activity of the protozoan grazers served as a "link" between the microbial loop and the classical food chain (Sanders and Porter, 1987), or as a "sink" for carbon (Ducklow et al., 1986). Various field studies, experimental results and modelling efforts have subsequently shown microzooplankton to be a link between the classical and microbial food webs in marine as well as fresh water bodies thus acting as conduits of energy and nutrients between the microbial level and higher trophic levels (Suttle et al., 1986; Frost, 1987; Cushing, 1995; Calbet and Saiz, 2005). Additionally, based on stoichiometric and biochemical grounds, microzooplankton, rather than phytoplankton, could be expected to be better prey for mesozooplankton (Klein Breteler et al., 1999; Broglio et al., 2003; Mitra and Flynn, 2005).

Today, the construction, testing and deployment of mathematical descriptions of plankton dynamics are central planks in marine ecology and climate change research. Most of these studies are based on the classic ecosystem model of Fasham et al. (1990). However, while over the last century our understanding of aquatic ecology has undergone a substantial change, models portraying these systems have not developed in line with field and laboratory observations. Model complexity has not typically increased in ecosystem

models to reflect improvements in our understanding of biological complexity with its attendant feedback mechanisms (e.g., Mitra and Flynn, 2007; Mitra and Davis, 2010; Rose et al., 2010). For sure ecosystem models have increased in complexity, but typically that complexity refers to numerical complexity; for example, 1-box representing the entire zooplankton (Z) community versus 3-boxes representing different zooplankton functional types (e.g., Franks, 2002 vs. Blackford et al., 2004). The dramatic increase in model complexity is almost wholly focussed on the phytoplankton-nutrient link, with regard to variables, processes and parameters. Very little, by comparison, has been done with the Z component; quite often employing only 2 classes (e.g., 78 P boxes vs. 2 Z boxes in Follows et al., 2007). Despite the plethora of mechanistic zooplankton models which have been developed over the past decade (e.g., Carlotti and Hirche, 1997; Carlotti and Wolf, 1998; Mitra, 2006; Mitra and Flynn, 2007; Flynn and Irigoien, 2009), the Z-boxes within ecosystem models are still biologically extremely simplistic with little or no differences in the physiological descriptions between the different Z-boxes.

The zooplankton community has thus been typically side-lined within ecosystem studies, not receiving the same level of importance as the phytoplankton and fish communities. Within biogeochemical models, zooplankton represent the top trophic level acting as a closure function, while within many fisheries models, zooplankton form the bottom level (see reviews by Plagányi, 2007; Carlotti and Poggiale, 2010; Fulton, 2010). There is a growing recognition of the need to bring together these two strands of research (biogeochemical and fisheries) through development of end-to-end ecosystem models combining physicochemical oceanographic descriptors with the biology of all trophic levels from microbes to higher-trophic-level, including humans, in a single modelling framework (Mitra and Davis, 2010; Rose et al., 2010). Figure 1 presents a conceptual model of such an end-to-end food web ecosystem. The zooplankton community (Z) acts as the conduit for the transfer of energy and material from the primary producers to the higher trophic levels and has a pivotal role in recycling and export of nutrients. Thus the zooplankton community is the critical link between biogeochemistry and fisheries (Carlotti and Poggiale, 2010; Mitra and Davis, 2010).

Here, we demonstrate the need to get the description of this Z-link correct, identifying the mismatch between our biological understanding and mathematical descriptions and thence proposing a guide for future

154 experimental as well as modelling efforts. As a justification for such work, we point to the need to find out
155 how various environmental and climatic factors may impact on ecosystem services important to humans
156 (e.g., fisheries). This requires a good understanding of the processes governing the functioning of the
157 ecosystems. This can be best achieved through an iterative process involving observations, experimentation
158 and modelling, in which inadequacies in any one component prompts renewed emphasis to make good those
159 identified short falls.

160 We commence by investigating the influence different vital rates and physiological functions have
161 on zooplankton dynamics. We then examine the experimental (field and laboratory) and modelling
162 approaches which underpin zooplankton research (especially related to the Z-vital rates) with an aim to
163 determine the level of mismatch in the two approaches. Using this information we provide a roadmap of how
164 the gaps between these two research strands may be narrowed such that the Z-link in end-to-end studies can
165 be configured more realistically. The findings from this work will act as a basis for the development of the
166 next generation ecosystem models which will aid understanding of the ocean ecosystem dynamics under
167 changing anthropogenic and climate events and thence inform various ocean management and policy
168 formulations through, for example, the EURO-BASIN project.

2. Zooplankton: definitions and vital rates

In order to parameterise the activities of the zooplankton, the Z-link in Fig. 1, we need to establish a working definition for zooplankton functional types. Over the decades, zooplankton have been classified into different types according to size (nano, micro, meso or macro), taxonomy, feeding strategy (e.g., ambush vs. suspension feeders; "herbivores" vs. carnivores), distribution (e.g., vertical, horizontal, geographical) and life-history strategies (e.g., broadcaster spawners vs. sac spawners). Here we classify zooplankton according to the aspects of their physiological functionality that are key for defining the link within end-to-end ecosystem studies, and how they are typically characterized in modern biogeochemical and ecosystem models (Table 1). The two main categories are the unicellular protists which we will refer to as microzooplankton (i.e., microbial zooplankton), and the multicellular zooplankton (i.e., all non-protists ranging from copepods to fish larvae), which we will refer to as mesozooplankton (i.e., all metazoans; thus this group includes the size classes of meso-, macro- and megalo-zooplankton).

Fig. 2 presents a schematic of the interrelationships between the vital rate processes of zooplankton. Many of these processes are common for both microzooplankton and mesozooplankton. One exception is food digestion; typically this occurs within a food vacuole in microzooplankton, and within a peristaltic gut for most mesozooplankton. However, one could argue that the digestive vacuole holding time in protists is analogous to gut transit time in, for example, copepods. The other clear exception is in the life cycle and reproductive process, which can be sexual and asexual in microzooplankton and is often by cell growth and simple binary fission, but involves a far more complex suite of processes in mesozooplankton.

3. Configuring the Z-box: sensitivity of Z vital rates to changes in the environment

Models are deemed to be *in silico* representatives of the real world. Arguably an ideal way to capture the dynamics of the zooplankton community, within end-to-end ecosystem models, water quality models, fisheries models (where Z are prey), earth systems models etc., is through incorporation of mechanistic descriptions of all the major physiological processes of the zooplankton functional types (Fig. 2; Table 1). In order to enable this, we would need a complete, biological and ecological, understanding of all those functions and how changes in the environment impact on the functionality of zooplankton as individuals as

195 well as a community. This would be a Herculean task. Aside from economic and time constraints, there are
196 numerous practical constraints which would hamper the attainment of the information (from experiments)
197 required to configure "perfect" zooplankton components. Even in instances where the physiological
198 parameters can be determined through experimentation, external forcings, such as seasonality, make snap-
199 shot data-sets biased. Given all these challenges, there is a need to identify which zooplanktonic processes
200 are the most significant (exert greatest leverage on the events) and warrant particular attention when linking
201 the biogeochemical models to higher trophic level models within any and all ecosystem models.

202 One way to identify these key processes is through conducting sensitivity analyses of models.
203 Sensitivity analyses of model structure are considered first at the level of the submodel (here, the
204 zooplankton) when operated in a steady-state situation (e.g., fixed prey quality and quantity; Mitra, 2006).
205 Having ensured that the model structure is not unduly sensitive, a dynamic sensitivity analyses (i.e., model is
206 operated in a dynamic, not steady state, setting) then has the scope to indicate which events in nature may be
207 considered of greatest "importance" and hence warrant particular attention to experimental and/or
208 observational research. Dynamic sensitivity analysis of a model is carried out for the purpose of checking the
209 behaviour of the model within its entire dynamic performance envelope. Thus a dynamic sensitivity analyses
210 of the Z-vital rate parameters used within food web and ecosystem models would demonstrate how robust
211 the model outputs are to changes in the "input" parameter values (e.g., assimilation efficiency) and thence
212 indicate the importance on ensuring the correct formulation and parameterization of these vital rate
213 descriptors.

214 Various modelling studies have looked at the impact (sensitivity), on food web and ecosystem models, of
215 using different response curve formulations (e.g., Holling vs. Ivlev) describing zooplankton physiological
216 functions, (e.g., Fulton et al., 2003; Anderson et al., 2010; Anderson et al., 2013). Here, however, we present
217 a dynamic sensitivity analyses on the zooplankton parameters (constants) which are used to formulate the
218 response curves to describe the zooplankton vital rates (e.g., maximum growth rate, assimilation efficiency)
219 within ecosystem and food web models. For this demonstration, we have used the Nutrient-Phytoplankton-
220 Zooplankton-Bacteria-Detritus (NPZBD) model of Fasham (1993). One may argue that this model (Fasham,
221 1993) is a simplified representation of the planktonic ecosystem and thence question whether the results from

222 the sensitivity analyses can be justifiably extrapolated to more complex ecosystem models. However, this
223 simplified description of the nutrient-phytoplankton-zooplankton interactions is employed widely forming
224 the basis of the plankton food web framework within ecosystems as well as fisheries models (e.g., Franks,
225 2002; Blackford et al., 2004; Follows et al., 2007; Plagányi, 2007; Rose et al., 2007; Rose et al., 2010;
226 Anderson et al., 2013). While the descriptions of the physics, phytoplankton and fish populations have
227 evolved to include varying levels of complexity (Fulton, 2010), the increase in complexity of the Z
228 descriptor has mainly been numerical (Mitra and Davis, 2010). While some models include additional
229 parameters like the impact of external forcings, such as temperature (e.g., Blackford et al., 2004), on the
230 zooplankton physical properties, such as movement (see reviews by Plagányi, 2007; Fulton, 2010), the main
231 description of the Z-vital rates follow the form of the Fasham (1993) descriptor. The vital rates of the Z
232 box(es) in ecosystems models, thus, is (are) still described as a form of the original Fasham (1993) equation:

233 $$\frac{dZ}{dt} = grazing - mortality - excretion$$

234 The parameters describing the Z vital rate processes within the Z-box in NPZBD type models are
235 identified in Fig. 2. It can be seen that each of the model parameters summarise a multitude of physiological
236 processes. For example, all the processes associated with the ingestion are summarised by two constant
237 parameters: the maximum grazing rate (G_{max}) and associated half saturation constant (K_{pred}); the processes of
238 prey encounter, detection, selection and capture are ignored. Likewise, the fate of incoming food (digestion,
239 assimilation, voiding, implications of variable gut transit time and associated variability in assimilation
240 efficiency) is summarised by a single fixed parameter, β (assimilation efficiency; in models with multiple Z-
241 boxes each of the Z functional types maybe assigned different constant β, e.g., Blackford et al., 2004; Fulton
242 et al., 2004), or ignored. Some processes, such as the feedback processes between the different vital rate
243 processes and those associated with age-stage developments, are not represented in the model at all. While
244 some ecosystem models do account for age-stage developments (see review by Carlotti and Poggiale, 2010),
245 it is notable that the feedback processes which drive biological systems are always ignored within food web
246 and ecosystem models. Other loss processes, such as mortality, are described as a closure function, which
247 represents a fixed loss to the higher trophic levels; mortality due to predation within the zooplanktonic

248 community (including cannibalism), diseases and old age are ignored. Knowledge of how sensitive these
249 parameters are to changes and also how robust the model is to changes in the parameters is, thus, a useful
250 first cut in revealing the importance of how the zooplankton physiological processes are incorporated within
251 models.

252 Traditionally sensitivity analyses are first conducted using single-parameter, steady-state tests, which
253 should identify overly-sensitive model components (Haefner, 1996). There are various studies which have
254 been conducted under steady-state conditions to gauge the sensitivity of the model parameters. These can be
255 broadly divided into two types, studies which investigate: (i) the sensitivity of the model structure; different
256 empirical descriptors are employed to describe a single process (e.g., use of Holling Type I vs. Type II vs.
257 Ivlev response curves to describe grazing) to see how these affect the model outputs and thence stability of
258 the steady-state system (e.g., Steele and Henderson, 1992; Edwards and Yool, 2000; Fulton et al., 2003;
259 Anderson et al., 2010), and, (ii) the sensitivity of the zooplankton community to changes in physical factors
260 such as turbulence (e.g., Fasham, 1995; Harms et al., 2000; Flynn, 2009).

261 We have, for the first time, conducted sensitivity analyses of the zooplankton vital rates model
262 parameters (Fig. 2 and Eq. 1) under dynamic conditions. Dynamic (non-steady-state) sensitivity analyses are
263 a more severe test of model behaviour, as the analyses indicate potential synergistic interactions within the
264 range of inputs and outputs that a model is likely to encounter and generate. Dynamic sensitivity analysis can
265 not only provide an indication of the relative sensitivity of each model parameter to fluctuations in the
266 parameter value, but any and all parameters can be considered simultaneously.

267 **4. Dynamic Sensitivity analyses: the process and results**

268 We conducted a dynamic (non-steady-state) sensitivity analysis of the zooplankton vital rate
269 parameters in the classic NPZBD model framework (Fasham, 1993) over a year-long simulation period.
270 Typically dynamic sensitivity analysis is conducted on the constants obtained from the process of fitting the
271 model to data; NPZBD model was tuned to the BioTrans dataset of phytoplankton, zooplankton, bacteria,
272 nitrate and ammonium for 47ºN 20ºW in the Atlantic (see Table 3 in Mitra, 2009 for the Z parameter values);
273 a detailed description of the BioTrans dataset is given by Lochte et al. (1993). The dynamic sensitivity

analyses were carried out using the "risk assessment" tool, in the modelling software, Powersim Studio, which employs a Latin Hypercube sampling method. The model was run 100 times with the values of the test parameters varied randomly around a mean value with an assigned distribution. The mean value for each test parameter was set as the value which gave the best fit to the data during the initial tuning process. All the parameters describing the zooplankton vital rates within the Z description in the NPZBD model were considered: grazing (G_{max}, K_{pred}), assimilation efficiency (β), excretion (ε), and mortality (μ_2 and K_6) (see also, Eq.1, and Fig.2). Variation for each parameter was assumed to follow a normal distribution around the optimal (tuned) value. In the absence of information to indicate the true variability of parameter values, in all instances, variation assumed a standard deviation of 10% of the mean (tuned) value. For the parameter describing assimilation efficiency (β), the variation was assumed to follow a truncated normal distribution (setting $\beta \leq 90\%$) since biologically it is not possible for the assimilation efficiency to approach 100%.

Fig. 3 shows the results from the dynamic sensitivity analyses on the modelled phytoplankton and zooplankton populations. From these plots can be gauged the sensitivity of the whole model behaviour, not just for zooplankton, to variation in the parameters controlling zooplankton vital rates. The parameters that have greatest potential for affecting the model behaviour were those describing grazing (G_{max}), assimilation efficiency (β) and mortality (μ). The values for parameters setting the half-saturation for predation (K_{pred}), excretion (ε) and the half-saturation for mortality (K_6) had no significant effect. It is noteworthy that the effects of variation in the configuration of the zooplankton component of the whole model were broadly of equal significance for the phytoplankton as for the zooplankton (Fig.3). When one considers the simplistic representation of the zooplankton vital rates in the NPZBD structure, that there is no consideration of prey quality and quantity and feedback processes on the vital rates, factors which have great impact upon zooplankton growth dynamics and thence on model output (Mitra and Flynn, 2005; Mitra, 2006; Mitra et al., 2007), then the need to improve our robust description of the functionality of models for zooplankton, as well as for parameter values is clear. Furthermore, here, and indeed in most plankton food-web models, the "Z" box encompasses all the different zooplankton functional types (Table 1), masking a range of ecologically important interactions (Mitra et al, 2007; Mitra, 2009).

In essence, the results of the dynamic sensitivity analysis (Fig. 3) demonstrate the importance of behaviour of the zooplankton component in models, of getting the model descriptions right. This applies not only for the zooplankton, but also for the phytoplankton and, by inference, for higher trophic levels that may be simulated as well. Having shown the critical importance of the modelled zooplankton vital rates, we now proceed to review the type and range of data available from experimentations (field and laboratory) and also the extant modelling efforts with a view to identify gaps in our knowledge for proper configuration of zooplankton models.

5. Physiological attributes of zooplankton *in vivo* and *in silico*

5.1. Feeding: detection, selection, capture and ingestion

Zooplankton diets are diverse, and can include ranges of prey sizes and types. When faced with multiple prey types, they typically demonstrate selective feeding. Feeding involves a series of processes that include prey (food) encounter, detection, selection, and capture leading to ingestion. Prey detection could be through usage of chemo- ("smell" and/or "taste") and/or mechano- ("feel") receptors and also depend on physico-spatial aspects such as swimming speed (of both prey and predator) and thence encounter rates and diffusion of chemical cues that in turn are affected by physical properties (e.g., turbulence).

315 **5.1.1. Field and laboratory studies of feeding**

316 Foraging takes place in a three-dimensional space with a patchy food distribution. Foraging effort
317 comes at an energetic cost to zooplankton and this must be balanced against food availability, its nutritional
318 quality and predation risk. Most species have developed adaptive behaviours and ontogenetic routines such
319 that their foraging strategies have emerged as an effort to optimize nutritional intake within their local
320 environment. These include daily and seasonal vertical migrations, adapting different swimming modes in
321 order to achieve a balance between avoiding mortality due to predation and enhancing encounter rates with
322 prey items (Osgood and Frost, 1994; Hays, 2003; Titelman and Kiørboe, 2003; Pierson et al., 2005) and even
323 jumping out of water (Gemmell et al., 2012). However, currently there are no available data to express the
324 dependence of the total metabolism of zooplankton on their swimming velocity such as there is for fish
325 (Brett, 1964).

326 In microzooplankton, although there are evidences of some sort of mechanoreception in ciliates
327 (Jakobsen et al., 2006), prey detection is most likely associated with a combination of chemical cues, such as
328 organics leaking from potential prey items, coupled with antibody-antigen type of surface recognition upon
329 physical contact (Martel, 2006; Menden-Deuer and Grünbaum, 2006). It has been suggested that if a prey
330 item turns out to be unpalatable, the protist predators can retain information about the physiological
331 condition of the prey type for a short period and therefore avoid it (Flynn and Davidson, 1993; Roberts et al.,
332 2011). Prey detection in non-protistan mesozooplankton, such as copepods (Poulet and Ouellet, 1982), krill
333 (Hamner et al., 1983), mussel larvae (Ward and Targett, 1989), siphonophores (Mackie et al., 1987) and fish
334 larvae (e.g., turbot and sole; Knutsen, 1992), also occur in response to “smell” from leaked organics from the
335 food item. Prey detection is further enhanced through physical perception using appendages specifically
336 adapted for mechano-reception (e.g., for copepods: Gill, 1986; for jellyfish: Mackie et al., 1987; Haddock,
337 2007).

338 Following detection, the zooplankton may or may not elect to capture the item. Using the various
339 combinations of prey detection mechanisms, most zooplankton (micro- and mesozooplankton) demonstrate
340 active prey selection distinguishing prey of different taxonomy (e.g., diatom vs. dinoflagellate; Tirelli and

341 Mayzaud, 2005), varying stoichiometry (within same species, e.g., *Oxyrrhis marina*, Flynn and Davidson,
342 1993, and between different species, e.g., *Acartia tonsa*, Jones and Flynn, 2005), live versus dead (e.g.,
343 *Paraphysomonas vestita*, Landry et al., 1991), natural versus artificial (e.g., ciliate *Strombidium*, Christaki et
344 al., 1998), and toxic versus non-toxic (e.g., copepods, Leising et al. 2005a; appendicularian *Oikopleura*
345 *dioica*, Lombard et al., 2011) prey items. Accordingly, zooplankton have been found to vary their feeding
346 modes (suspension vs. ambush, Saiz and Kiørboe, 1995) switching between prey items, across different
347 trophic levels, with changes in abundance (e.g., copepod, Castellani et al., 2005a; krill, Onsrud and
348 Kaartvedt, 1998; Lass et al., 2001; Agersted et al., 2011) and prey nutritional status (Flynn and Davidson,
349 1993; Jones and Flynn, 2005).

350 Prey thus selected may still not be captured and ingested; indeed, all captured prey are not
351 necessarily ingested. For example, Tong (1997) observed the microzooplankton *Paraphysomonas vestita* to
352 capture prey and then either ingest them or reject them with a flicking action of its flagella; *Mesocyclops* has
353 been observed to reject larger cladoceran prey such as *Bosmina longirostris* and *Scapholeberis mucronata*
354 post-capture and pre-ingestion (Chang and Hanazato, 2005). Copepods have been shown to "feel" the
355 captured prey before deciding whether to ingest or reject it (Paffenhöfer and Van Sant, 1985). Prey capture
356 and ingestion may be influenced by allometrics (prey:predator size ratio), taxonomy and/or prey (chemical or
357 elemental) stoichiometry (i.e., quality). Unsurprisingly, prey quantity has an overarching impact; the impact
358 of allometrics and stoichiometrics on prey capture and ingestion is accentuated by extreme prey abundance
359 (high and/or low). Copepods, when confronted with high prey: predator size ratios or with long diatom
360 chains, have been found to be inefficient at the point of prey capture, demonstrating what is termed "sloppy
361 (messy)" feeding (Corner et al., 1972; Møller, 2005; Møller, 2007). In contrast, zooplankton, such as pelagic
362 tunicates, which are primarily filter feeders, appear to ingest food mainly as a function of numeric density
363 and size, with typically no impact of food nutritional quality.

364 How zooplankton feed impacts on trophic dynamics in different ways. For example, superfluous
365 feeding by mesozooplankton, resulting in the production of high densities of undigested faecal material
366 subsequently lost from the pelagic waters, could support the benthic community (Beklemishev, 1957; Fig. 1).
367 Sloppy feeding by copepods, releasing substantial amounts of dissolved organics in to the pelagic waters

(Cushing and Vućetić, 1963; Møller et al., 2003; Møller, 2005), and "messy feeding" by krill only ingesting part of copepod prey (e.g., limbs, copepod soft part) leaving behind the entire copepod-carcass intact (Ohman, 1984; Båmstedt and Karlsson, 1998), could be advantageous to the microbial community.

Furthermore, there is the issue of which prey types are being eaten and the allied consumption rates; this will have a direct effect on the prey community structure and abundance. For example, preferential grazing on certain phytoplankton species by zooplankton may promote production of algal, especially harmful or toxic, blooms on one hand (Pierson et al., 2005; Gismervik, 2006; Mitra and Flynn, 2006a; Ribalet et al. 2007) and on the other hand have been found to be capable of controlling established algal blooms (Calbet et al., 2003; Jeong et al., 2010). Certain zooplankton may continue feeding on toxic blooms (copepods, Halsband-Lenk et al. 2005; krill, Bargu et al., 2003) with deleterious effects on not only their own fitness but also that of the next generation (Colin and Dam 2002, Halsband-Lenk et al. 2005). In contrast, intraguild grazing within the zooplankton community, releasing phytoplankton from grazing pressure, may induce trophic cascades (e.g., copepods grazing on microzooplankton community, Leising et al., 2005b).

The available literature, thus, demonstrates the complexity and diversity in zooplankton feeding mechanisms and associated impacts from and on the environment. However, there are several caveats. The data available from experiments are for a limited range of zooplankton (typically female copepods) and associated prey types (see Table 2). Also, often the experiments are conducted under unnatural conditions (e.g., constant environments, high nutrient status). The data obtained are then typically fit with *a priori* functions that may not depict the correct relationship.

5.1.2. Modelling descriptions of feeding

Studying detection, capture and ingestion is non-trivial because of the rapidity of the interactions and the feedback from the accumulation (and then digestion) of ingested material. There is no single zooplankton model which encapsulates the full inter-relationship between the different mechanisms governing zooplankton feeding. Within ecosystem models (such as NPZBD, Fig. 2), zooplankton feeding is typically described through a single zooplankton functional response curve (e.g., the Holling Types, Ivlev curve;

394 Gentleman and Neuheimer, 2008; Anderson et al. 2010). The biological descriptors of the Z vital rates are
395 thus lumped into a single process (typically defined through parameters akin to G_{max} and K_{pred} in Fig. 2) and
396 the feedback mechanisms between these processes, innate to biological systems, are ignored. This problem is
397 analogous to that for nutrient transport and initial assimilation (collectively being "uptake") in studies of
398 phytoplankton nutrition (Flynn, 1998). However, what these models do demonstrate is that the incorporation
399 of even biologically simplistic formulations of grazing have the potential to destabilize the system or predict
400 very different population dynamics.

401 There are various modelling efforts investigating the different processes associated with zooplankton
402 feeding. For example, there are a suite of models which explore the foraging strategies of zooplankton
403 (Leising and Franks, 2000; Leising et al. 2005c; Morozov et al. 2011); however, similar to the grazing
404 descriptions in NPZ-type models, these models also focus on the impact of employing a single equation but
405 of different mathematical forms to describe the foraging strategies. Visser (2007) presented a detailed model
406 describing the different physical chemical processes associated with zooplankton feeding and survival
407 strategy highlighting the importance of considering these processes. There are various models describing
408 prey detection and capture based on zooplanktonic swimming behaviour (e.g., Leising, 2001) and predator-
409 prey encounter rates (e.g., linear swimming, Gerritsen and Strickler, 1977; random-walk swimming, Evans,
410 1989). These models tend to be dominated by theoretical considerations with little or no parameterisation to
411 experimental data. However, Kiørboe and Saiz (1995) proposed mechanistic models describing the dynamics
412 of mesozooplankton prey detection and capture efficiency; they constructed and parameterised their models
413 using experimental data.

414 Selection between prey items is a complex biochemical/physiological suite of functions. In models
415 this activity, which can be critical for system dynamics, has typically been modelled poorly. There are
416 numerous ad-hoc prey selectivity functions which have been used as a front-end for zooplankton models (see
417 review by Gentleman et al., 2003). Most of these selectivity functions group together the processes of prey
418 detection, selection and switching using fixed constants to formulate the response curves. They typically do
419 not take into account the singular or synergistic impact of prey quantity and quality on feeding as observed in
420 nature. Nor do they enable adaptive prey switching or differentiate between contrasting ingestion kinetics of

different prey types. Moreover, most of them result in modelled feeding behaviours that are suboptimal, for example, ingestion rates that decrease when food availability increases. Clearly, there is a need to improve these types of characterizations.

Mitra and Flynn (2006b) presented a selectivity function based on experimental findings that enables active prey selection allowing the zooplankton to switch to alternate prey types when there is a decline in prey (stoichiometric) quality and/or quantity; prey preference can be made to vary with prey quality and quantity. The ultimate control within this function is not the external concentration of each or the total prey (as typically used in ecosystems models), but is a function of the rate of prey capture relative to predator demand and the amount of ingested prey within the predator gut. Hence, if required, any/all prey can be deselected, or the impact of inert materials or turbulence adversely affecting capture rates of any or all prey can be considered. Fig. 4 demonstrates the potential for this selectivity function to describe experimental results compared to traditional approaches.

5.2. Food processing: gut transit time, digestion, assimilation and voiding

Ingested material is either wholly or partially digested, and the unassimilated fraction is voided (Fig. 2). Digestion refers to the breakdown of ingested material for incorporation (assimilation) into the consumer body; digestion hence commences at the point of ingestion or during preliminary food crushing during prey handling, terminating with defecation of undigested material (though some level of post voiding digestion, associated with continued enzymatic activity and bacteria-mediated decay will likely occur). The processes of ingestion, digestion, assimilation and voiding are not independent of each other but are related through various internal feedback processes (Mayzaud et al., 1998) and depend on the quantity and quality of prey within the digestion vacuole or gut (Mitra and Flynn, 2005). Various studies have demonstrated that the stoichiometric (quality) differences between the predator and ingested prey impacts on the digestion efficacy, the retention of the ingestate within the digestive tract (vacuole for protists) and therefore on assimilation efficiency (Tirelli and Mayzaud, 2005; Mitra and Flynn, 2007). The efficacy of these processes in turn impact on the trophic dynamics through the defecation and/or excretion (including regeneration) of material (Darchambeau et al., 2003). For example, the nature of the voided material affects not only the trophic levels

447 above the zooplankton, but also those below. Thus, voided organic matter will drive the microbial loop
448 (Landry 1993, Ducklow et al., 2002, Calbet and Landry, 2004). Likewise, food quality has an impact on the
449 size and density of faecal pellet production. *Acartia tonsa* when fed on ciliate and diatom diets have been
450 observed to produce larger pellets resulting in fast estimated sinking rates (Feinberg and Dam, 1998) causing
451 loss of material from the photic zone. As a result any inorganic nutrients ultimately liberated by microbial
452 action on the voided organics will not necessarily be in the appropriate place or time frame to support algal
453 growth.

454 **5.2.1. Field and laboratory studies of food processing:**

455 In protists digestion occur external to the main cell, or internally within digestive vacuoles (Öpik and
456 Flynn, 1989; Hansen and Calado, 1999). External digestion may involve usage of a membranous feeding veil
457 (e.g., thecate dinoflagellates, Jacobson and Anderson, 1986), or a peduncle to spear the prey and then ingest
458 the digestate back through the peduncle (Hansen and Calado, 1999); such adaptations enable
459 microzooplankton to consume prey items that are bigger than themselves. Most non-protist zooplankton, in
460 contrast, possess a digestive tract (gut) through which the ingested material passes and is digested by
461 enzymes secreted by the different cell types lining different sections of the gut. A major advantage possessed
462 by some protistan microzooplankton is their body plasticity. They have been found to accommodate food
463 vacuoles all over the body (Öpik and Flynn, 1989, Roberts et al., 2011), increasing the initial body volume
464 several times (Calbet pers. obs.; Hansen, 1992), or engulf large prey, such as diatom chains, several times
465 their own body size (Nakamura et al., 1995; Saito et al., 2006; Calbet, 2008). The metazoan gut, in contrast,
466 does not have such flexibility, though with some exceptions in the Cnidaria and Ctenophora phyla (Haddock,
467 2007; Pagès and Madin, 2010).

468 The period for retention of the ingested material within the digestive apparatus varies among
469 microzooplankton. For example, *Oxyrrhis marina* has been observed to take as long as 3 days to complete
470 digestion of a single meal (Öpik and Flynn, 1989), while the digestion time of the heterotrichous marine
471 ciliate *Fabrea salina* has been found to be ca. 71 minutes when presented with different prey concentrations
472 (Capriulo and Degnan, 1991). In mesozooplankton the gut passage time (equivalent to the food vacuole

processing time in a protist) is much faster in absolute terms (e.g., ~0.3 and 6 hours Besiktepe and Dam, 2002). The time it takes for the ingested material to pass through the gut is a function of the stoichiometric quality of the ingested prey as well as the quantity of food available in the environment. For example, the gut passage time of a mesozooplankton may increase (i.e., ingestate is held longer) in the presence of poor quality food to enable thorough digestion of the ingested material (e.g., Horn and Messer, 1992; Plath and Boersma, 2001). Alternatively, the gut passage time may decrease with low food quality or high food availability (Tirelli and Mayzaud, 2005; Dutz et al., 2008) and thence demonstrate density dependent inefficiency (Flynn, 2009). Such events are not unique to mesozooplankton, but occur across higher trophic levels such as yellow-rumped warblers and harbour seals (Afik and Karasov, 1995; Trumble and Castellini, 2005). In addition to the variability introduced by food quality and/or quantity, the gut transit time is also likely to be sensitive to incubation temperatures (Irigoien, 1998); one may expect protist food vacuole processing times to be similarly affected.

Even with optimal food quality in abundant quantity, digestion and assimilation for any organism can never attain 100% efficiency. The assimilation efficiencies of micro- and meso-zooplankton have been found to vary widely from being as high as 60-95% to lower values of 10-20% (Landry, 1993; Thor and Wendt, 2010) dependent on food quality and quantity. At higher food concentrations, mesozooplankton are least efficient at assimilation (Corner et al., 1972; Head, 1992; Tirelli and Mayzaud, 2005; Thor and Wendt, 2010). The relatively lower assimilation efficiency observed in mesozooplankton compared with that of a microzooplankton may be attributed to the presence of a gut in the mesozooplankton and thus the inevitability of voiding material associated with the peristaltic gut functioning.

Low assimilation efficiency at high food availability does not adversely affect the individual grazer (though in time it may well affect the population). The critical issue is to maintain a high gradient of nutritional components across the gut wall, and that is best attained by having the gut packed with only partly digested food, rather than retaining food and extracting every last useful molecule from it. Lehman (1976) reported that 95% of the demand could be met by a gut only 30% full. The activity does, however, have great potential for affecting ecosystem dynamics as the end product of the digestion/assimilation process would

499 vary markedly (e.g., dense vs. loosely packed faecal pellets) depending on the rate of flow of ingested
500 material through the gut (Mitra and Flynn, 2007; Flynn, 2009).

501 Due to biochemical constraints a consumer has to get rid of material in excess of what it requires for
502 immediate use, for growth and (as applicable) for accumulating reserves such as oil. Thus food that is
503 ingested and not assimilated is egested (voided). There is a suggestion that some zooplankton may "burn off"
504 surplus ingested carbon (Darchambeau et al., 2003). However, this evidence comes from studies on *Daphnia*,
505 which typically feed indiscriminately on phytoplankton species that accumulate excess carbon in the form of
506 starch rather than lipid (such as in copepods feeding on diatoms). Lipid is less easily digested and
507 metabolised compared to starch, so the respiration rate associated with "burning off" lipid will be relatively
508 higher than when using starch. However, excess C (especially in the form of sugars) in the diet could
509 conveniently compensate for the additional costs in hunting alternative, high quality, food.

510 Voided material includes particulate and dissolved organic components and their distribution
511 depends on numerous factors including the balance of digestion and assimilation of ingested material, the
512 gut/digestive vacuole transit rate, and the packaging of the faeces. For example, copepods may exhibit a
513 short gut residence time coupled with high ingestion rates if food concentrations are high (Dagg and Walser,
514 1987) resulting in voiding of part-digested material. Such faecal pellets may sink and enter the benthic food
515 web or may act as food for other copepods in the pelagic zone. Partly digested material has been found to act
516 as food for mesozooplankton (Mauchline, 1998), as well as for microzooplankton (e.g., *Oxyrrhis marina*,
517 Flynn and Davidson, 1993; *Gyrodinium dominans*, *Gyrodinium spirale*, *Diplopsalis lenticula*,
518 *Protoperidinium depressum*, Poulsen et al., 2011), and some mixotrophic dinoflagellates in the absence of
519 alternative prey items (*Karlodinium armiger*, and a gymnodinoid dinoflagellate, Poulsen et al., 2011). Some
520 diatoms may pass through the gut of a zooplankter and upon defecation may still remain viable (Van Donk et
521 al., 1997; Peterson and Jones, 2003). This is not singular to diatoms; subitaneous eggs and resting eggs of
522 copepods have also been found to remain intact and viable after passage through fish guts (Bartholme et al.,
523 2005); likewise cyanobacteria, such as *Synechococcus*, have also been found to be intact and viable after
524 passing through the gut of appendicularians (Gorsky et al., 1999).

525 **5.2.2. Modelling descriptions of food processing**

526 Traditionally consumer models are ingestion controlled for applications in ecology, or digestion
527 controlled for use in aquaculture and animal husbandry (Mitra and Flynn, 2007). Rarely do they have an
528 integrated representation of variable ingestion kinetics, digestion efficiency, and/or gut transit time with
529 changes in food quality and/or quantity. Zooplankton models are typically ingestion controlled, with the
530 primary, if not sole, kinetic interface being at feeding. Thus, for example, a fixed value for assimilation
531 efficiency, irrespective of variations in food types, is typically assumed (akin to same maximum grazing rate
532 assumed for all food types). Even where food quality is considered, this is related to stoichiometric
533 differences between zooplankton and food at the point of assimilation and assimilation efficiency is typically
534 assumed to be fixed (e.g., Sterner and Elser, 2002; Anderson et al., 2005).

535 If the food ingested is of poor nutritional value, a predator that possesses a gut has two options: (i)
536 defecate it as fast as possible (with a high gut passage time), maintaining a high cross-gut membrane
537 metabolite concentration and so increase the likelihood of absorption of compounds of value or, (ii) retain
538 the food for a longer duration (with a low gut transit time) and thus ensure that digestion of the material is as
539 complete as possible (Mitra and Flynn, 2005). In the former instance, the short gut residence time support a
540 high ingestion rate and low assimilation efficiency. In the latter, the rate of assimilation would act as a
541 feedback on ingestion slowing it down or even stopping it (Dagg and Walser, 1987) while assimilation
542 efficiency is increased. These processes are modelled by Mitra and Flynn (2007), who presented a generic
543 model for consumers with a gut describing the linkages between ingestion, digestion, assimilation and gut
544 transit time as functions of food of varying quality and quantity. This model was validated against
545 experimental data sets for marine copepods and freshwater cladocerans grazing on phytoplankton of different
546 quality (i.e., N:C and P:C) and quantity.

547 While experimental work shows the very real potential for variations in digestion dynamics to affect
548 assimilation efficiency, these lines of evidence are not reflected by typical zooplankton models used in
549 ecosystem studies. These continue to couple overly simple descriptions of feeding kinetics to, at best,
550 stoichiometric-linked digestion functions with fixed assimilation efficiency. It is perhaps worth noting that

possession of a high assimilation efficiency is not itself important to a consumer. The critical issue is the rate of transference of metabolites across the gut wall; there is in reality an important interaction between that driver, assimilation efficiency and ingestion rates (Mitra and Flynn, 2007) and thence to trophic dynamics (Flynn, 2009).

The form of voided material, the balance between POM and DOM, is typically either not modelled or assumed as a fixed ratio. In reality, it will vary with the nature of the food, with the predator type, and with gut transit time. This partitioning has important implications for trophic dynamics; POM may sink and represent food for other zooplankton while DOM is a resource for the microbial loop.

5.3. Excretion: respiration and nutrient regeneration

5.3.1. Respiration

Respiration is required primarily to support the maintenance of homeostasis and to repair systems. Collectively these constitute basal, or resting, respiration. In addition there is respiration associated with anabolism, catabolism, net metabolism, growth and movement (e.g., swimming, vertical migration associated with prey capture and predator avoidance). Classically, interest in the respiratory rates of zooplanktonic organisms has been stimulated by interest in quantifying the energy requirements of copepods (as important representatives of the zooplankton community) and productivity of marine ecosystem and thence to gain a better understanding of ocean carbon cycling (Hernandez-Leon and Ikeda, 2005). Overall, there is more information on respiration rates of planktonic copepods and crustacean in general; very little is known about other zooplankton taxa (Ikeda et al., 2001; Hernandez-Leon and Ikeda, 2005).

Respiration is often hypothesized to be higher for organisms with small cell size and vice versa; as a result measurements of respiration are made as functions of the cell size. However, this does not necessarily hold true in all instances. The physiological state of the cell and environmental conditions has been shown to be of vital importance in ascertaining respiratory rates (Fenchel 2005). Figure 5 (recreated by transformation of data from Fenchel 2005) demonstrates how the respiration rates of four different groups of microzooplankton change under food replete and deplete conditions. While under prey-replete conditions the

576 "cell size" hypothesis appears to hold true, under prey deplete conditions, the respiration rates of the four
577 groups appear to be more or less similar. Thus, it is prudent to take into account the physiological state of the
578 cell and environmental conditions and not just the cell size during measurement of respiration rates.

579 **5.3.1.1. Field and experimental studies for respiration**

580 In poikilothermic organisms, such as zooplankton, respiration rate is considered to vary mainly as a
581 function of body size and temperature (Peters, 1983; Ikeda et al., 2001) and a simple equation has been
582 proposed to describe the metabolic rate of all organisms from "first principles", using a combination of body
583 mass scaling and classical statistical thermodynamics (Gillooly et al., 2001; Brown et al., 2004). In
584 particular, the scaling of metabolic rate with body mass has long been a controversial topic (Gillooly et al.,
585 2001; Brown et al., 2004; Glazier 2006; Kolokotrones et al 2010; Glazier 2010). Since the seminal work of
586 Kleiber (1932) and Hemmingsen (1960) it has been generally assumed that the metabolic rate of most
587 organisms, including animals, plants, and unicells increases as the body mass to the power ¾ (i.e.
588 0.75), intermediate proportionality between body weight and surface (Kleiber 1932, Hemmingsen
589 1960, Brown et al. 2004). The search for an explanation for this apparent universal exponent has led
590 several authors to argue that the ¾ metabolic scaling is the result of has been explained as being the
591 result of the physical properties of internal resource–transport networks present in organisms,
592 including the circulatory and respiratory systems (West et al., 1997; Banavar et al., 2010; West and
593 Brown, 2005). However, recent theoretical and empirical research has questioned the 3/4-power law
594 and the resource–transport network (RTN) models proposed to explain it, by showing that such
595 models are based on questionable or unsubstantiated assumptions (Glazier 2009; Kolotrones et al.
596 2010; Agutter and Tuszynski 2011). For instance, in a recent study, Kolotrones et al. 2010 have
597 shown that the relationship between metabolic rate and body mass has a convex curvature on a
598 logarithmic scale suggesting that this metabolic coefficient is highly sensitive to the body mass
599 range used. Moreover, several comparative surveys of various animals and plants have
600 demonstrated that intra- and interspecific values of the metabolic scaling often differ significantly

601 from 3/4, varying from approximately 2/3 to 1 (e.g., Bokma 2004; Glazier, 2005, 2010; White et al.
602 2006 and 2007; Isaac and Carbone, 2010). Furthermore, recent studies suggest that the intraspecific
603 metabolic-scaling exponent may be related to various ecological factors, including zooplankton
604 activity, habitat, and temperature (Glazier 2005, 2006 and 2010). For instance Glazier (2006)
605 reported that isometric scaling i.e. a metabolic scaling of 1, appears to be common in planktonic
606 animals and argued that it probably represents an adaptation to the high-energy cost of continual
607 swimming to stay afloat, rapid growth rates and reproductive rates in response to high levels of
608 mortality in open water.

609 Other factors such as food availability, food quality and temperature acclimatisation also affect
610 respiration (Conover and Corner, 1968; Butler et al., 1970; Kiørboe et al., 1985; Fenchel, 2005; Gaudy and
611 Thibault-Botha, 2007; Castellani and Altunbaş 2013). In addition, respiration rates vary between species and
612 also within a species throughout the growth phase (Fenchel and Finlay, 1983; Kiørboe et al. 1985).
613 Respiration rates also depend on various physical factors such as swimming, turbulence and temperature in
614 conjunction with the quantity of available food. At saturating food concentrations, zooplankton demonstrate
615 high respiration rates a phenomenon known as Specific Dinamic Action (SDA) (Kiørboe et al., 1985).
616 However, a decline in food availability often initially results in an increase in predatory activity; respiration
617 increases with increasing swimming activity reaching a maximal value till starvation and fatigue sets in
618 (Hernández-León and Ikeda, 2005). This increase may be further accentuated under high turbulence where
619 the predator cannot easily find prey (Kiørboe and Saiz, 1995). Under starved conditions, zooplankton would
620 be expected to only utilize energy necessary for survival resulting in low respiration rate values (Kiørboe et
621 al., 1985). The increase in respiration rate of fed copepod, i.e. SDA, has been shown to depend largely on
622 protein biosynthesis (i.e. to growth and reproduction) and protein metabolism, rather than on the mechanical
623 filtering and ingestion of the food (Kiørboe et al. 1985, Clarke and Fraser 2004, Secor 2009). Hence, several
624 authors have proposed that seasonal changes in the oxygen consumption of poikilotherms including marine
625 copepods could reflect seasonal changes in their growth and reproductive rates (Parry, 1983; Clarke, 1993;
626 Castellani and Altunbaş, 2013). Results of a recent laboratory study have also shown that copepod

627 respiration rate varies significantly with the quality of the food ingested probably as a result of changes in the
628 biosynthetic activity of the organism (Nobili et al 2013).

629 **5.3.1.2. Modelling descriptions for respiration**

630 Steele and Mullin (1977) split respiration into three parts, (i) basal, (ii) foraging and/or capture cost,
631 and, (iii) cost of transforming and assimilating food. The last two categories are often grouped as active and
632 within models classed together as metabolic costs. Thus, typically respiration in (individual-based as well as
633 ecosystem) models is considered as two components, basal and metabolic. Basal respiration is that part
634 which is necessary for the survival of an organism; this includes all essential functions. Metabolic respiration
635 costs occur in conjunction with metabolic functions (e.g., assimilation). It should be noted that what is
636 usually measured experimentally is routine metabolism (i.e., basal+active) of starved organisms as it is
637 physically difficult to separate these out. Models typically do not attempt to replicate changes in respiration
638 rate with a down-turn in food availability, as observed in nature (see above). A major impediment in the
639 translation of empirical data to models is the basis of respiration measurements. Too often this relates oxygen
640 consumption to animal size (length) while models typically require units as C C^{-1} d^{-1}.

641 The impacts of temperature on respiration rates are described further below within (5.6).

642 **5.3.2. Nutrient regeneration**

643 Zooplankton ingest food in the organic form, i.e., nutrients such as nitrogen, phosphorus etc. are
644 present in combination with carbon. A proportion, perhaps the bulk, of these elements is
645 regenerated/excreted during catabolic respiration (Landry, 1993; Fenchel, 2005). We define this process of
646 loss of nitrogen, phosphorus and others (notably iron, Fe) by the zooplankton in order to maintain its
647 stoichiometric balance against the loss of carbon through respiration as nutrient regeneration.

648 **5.3.2.1. Field and experimental studies of nutrient regeneration**

649 Regeneration of nitrogen (N) by the protist *Paraphysomonas* sp. has been observed to be low during
650 starvation (Goldman and Dennett, 1992), consistent with the observed low (basal) respiration rates under
651 similar conditions (Fenchel, 2005), while regeneration as well as respiration rates have been reported to be

652 substantially higher during the active grazing phase. N, typically regenerated as ammonium (NH_4^+) during
653 catabolism, cannot be accumulated in the zooplankton body (Hasegawa et al., 2001) but has to be excreted
654 due to its toxic nature. This excreted NH_4^+ then supports phytoplankton production (Park et al., 1986; Bode
655 et al., 2004). Phosphorus is typically released as phosphate (PO_4^{3-}) during catabolism, which unlike
656 ammonium is not toxic and can be readily recycled internally.

657 **5.3.2.2. Modelling descriptions of nutrient regeneration**

658 Within classic N-based NPZ models (which do not describe carbon dynamics), nutrient regeneration
659 is typically assigned a fixed constant; i.e., it is assumed that a fixed proportion of the ingested material is
660 always excreted as ammonium (e.g., ε, Fig. 2). In multi-element models N and P are regenerated to maintain
661 (fixed) stoichiometric content of the zooplankton. Thus, for example, Mitra and Flynn (2007) describe
662 nutrient regeneration as a function of the quality of ingested material. There are clear implications for trophic
663 interactions if the prey stoichiometry is significantly poorer than that of the consumer (e.g., $N:C_{prey} <$
664 $N:C_{predator}$). In such situations there is less release of N to support the next generations of phytoplankton,
665 leading to a further deterioration in prey quality (i.e., low N:C) which in turn leads to rejection of the low
666 N:C phytoplankton by the zooplankton predator (Flynn and Davidson, 1993), resulting in a noxious
667 phytoplankton and/or toxic algal bloom (Turner and Tester, 1997; Mitra and Flynn, 2006a). What is lacking
668 in typical models of zooplankton, however, is a variable C:N:P ratio (e.g., for copepods storing lipids, Miller
669 et al., 2000). Such events would affect nutrient regeneration both during lipid deposition and during
670 consumption (respiration) of that lipid.

671 **5.4. Zooplankton growth: growth and life cycles**

672 Growth of the zooplankton is a function of ingestion, assimilation and the various loss processes.
673 Life history strategies evolved as adaptive mechanisms to optimize zooplankton survival and proliferation
674 and vary between constant environments and more unpredictable, seasonal environments (Allan, 1976).
675 Unique combinations of life history strategies, metabolic demands, and physiological performance determine
676 the structure of pelagic food webs in an interplay of bottom-up processes (resource availability) and top-
677 down control (predatory interactions) (Verity and Smetacek, 1996). During the life cycle of protist

678 zooplankton allometric changes are limited to the approximate doubling and halving of cell size. For non-
679 protist zooplankton however, the range of organism size over the life cycle may cover many tens, hundreds,
680 or even thousands of orders of magnitude. With this there are important allometric scaling events for every
681 process mentioned previously (Atkinson and Hirst, 2007).

682 Associated with growth is development. The two processes of growth and development are
683 decoupled on one hand but interdependent on the other. Thus, growth can be negative but development
684 cannot. Likewise development can be arrested if growth is not at a critical level.

685 **5.4.1. Field and experimental studies of growth and life cycles**

686 Because of the impracticability of measuring growth in the field over days and weeks, most field
687 studies make snap-shot studies of individual growth rate (physiological) processes, and extrapolate these to
688 estimate overall growth rates. The determination of growth rate from weight specific copepod egg production
689 rate (i.e., egg gC female gC^{-1} d^{-1}; e.g., Kimmerer and McKinnon, 1987; Berggreen et al., 1988) or through an
690 exponential model fit are prime examples. Even for microzooplankton, which may have generation times of
691 around a day, growth rates are not determined by increases in whole organism biomass. Only in mesocosms
692 may whole life cycles be followed. In consequence, there are remarkably few studies of zooplankton growth
693 over a prolonged period where changes in C, N, P biomass has been followed, in addition to age and size-
694 structure, as is required to properly test and validate models. Where growth rates have been estimated from
695 experimentation, the methods of estimation (specifically for copepods) have received significant criticism
696 (Hirst et al., 2005).

697 All organisms have a maximum possible growth rate at a specific temperature, and an absolute
698 maximum possible growth rate, though for long-lived species the optimum temperature may differ for
699 each/with age class. This maximum growth rate can be achieved when good quality food is present in high
700 quantity in the environment such that there is an excess of nutritious ingestate within the zooplankton
701 digestive vacuole/gut after accounting for all the losses incurred by the predator (i.e., respiration,
702 regeneration etc.). A zooplankter may optimise its growth rate through enhancing its assimilation rate by
703 altering its rates of ingestion, gut transit and/or voiding (Mitra and Flynn, 2005) depending on the quality and

quantity of prey available (see above). However, in reality, typically it may not be possible to reach the absolute maximum rate due to the lack of sufficient food, competition for resources between different organisms, presence of unfavourable food in nature and/or unfavourable physical and/or chemical conditions (e.g., pH, temperature, salinity).

For survival in food limiting conditions, zooplankton may resort to consumption of storage lipids (Lee et al., 2006) or to different survival strategies such as formation of resting spores or cysts (microzooplankton: Rubino et al., 2000; hydrozoa: Boero et al., 2008) and diapause (copepods: Mauchline, 1998). Many species of the *Calanus* genus undergo a resting-phase, usually during the CV copepodite stage (Miller et al., 1991; Hirche, 1983; Heath and Jónasdóttir, 1999). During the winter months, when there is a shortage of food in the surface waters, the CV copepodites vertically descend into deeper colder water (200-2000m). Here it is believed they enter into a state of diapause where they cease to feed and have a decreased metabolic rate and respiration (Hallberg and Hirche, 1980; Ingvarsdóttir et al., 1999). Diapause has been defined as a programme of arrested development or ontogeny coupled with physiological changes to ensure survival through adverse environmental conditions, it is not however an immediate response to the result of these unfavourable conditions, but rather, is cued by some factor that normally precedes the deterioration of these environmental factors, and is ultimately genetically determined. During periods of food satiation, *Calanus* accumulates lipid, mostly in the form of wax esters along their prosome (Miller et al., 2000). These lipid reserves are thought to be used not only as an energy store throughout the non-feeding period, but also for gonad development and reproduction in spring (Tande, 1982; Richardson et al., 1999). Recent research proposes a new perspective on the role of lipids in zooplankton, suggesting that solid-liquid phase transitions of lipids are factors regulating their buoyancy and also controlling the life cycles of calanoid copepods that diapause (Pond and Tarling, 2011; Pond, 2012). Many calanoid copepod species also produce diapause resting eggs that lie dormant in the benthos when the environmental conditions are unfavourable for development (Grice and Marcus, 1981; Engel and Hirche, 2004). While copepods typically form diapause eggs, encystment has also been observed in the marine copepod *Heteropsyllus nunni* (Coull and Grant, 1981).

730 In the event of declining food availability zooplankton may decrease their respiration rate resulting
731 in a decline in the carbon turnover preventing the organism from respiring itself to death (Fenchel, 2005).
732 However, the respiration rate can only decline to a certain minimal value; if unfavourable conditions persist,
733 the organism would form cysts and as there are no (or minimal) respiratory or excretory losses associated
734 with cysts or diapause eggs they can thus remain viable for long periods of time. Excystment and hatching
735 occurs in the advent of favourable conditions and, after a lag phase (required for revitalization of the enzyme
736 system), the organism starts to prepare for growth/division/reproduction (Mauchline, 1998; Fenchel, 2005).

737 To optimize the timing of life cycle traits, such as growth, reproduction and dormancy, many species
738 synchronize their physiology to environmental clues. Many examples for polar and temperate settings are
739 available, especially for copepods, and range from highly seasonally tuned ontogenetic cycles at high
740 latitudes (e.g., Conover and Huntley, 1991; Schnack-Schiel, 2001) to continuous life cycles with many
741 generations per year (e.g., Halsband and Hirche, 2001; Halsband-Lenk et al., 2004).

742 **5.4.2. Modelling descriptions of growth and life cycles**

743 Growth rates, and specifically maximum growth rates, are key parameters in zooplankton models.
744 However, in classic NPZ models (e.g., Fasham et al., 1990) as typically used in ecosystem studies,
745 zooplankton growth is limited (fixed) by the parameter defining the maximum grazing rate (G_{max} in Fig. 2).
746 Maximum growth rate in these models is, therefore, a function of grazing kinetics, offset by a series of
747 constants summarising assimilation, voiding and regeneration, with no recognition of any of the internal
748 feedback processes that occur in reality.

749 Most models of zooplankton life cycles focus on calanoid copepods, including key species of the
750 *Calanus* complex. They range from conceptual descriptions based on seasonal or multi-annual field sampling
751 (Peterson, 1999; Halsband-Lenk et al., 2004) to individual- or stage-based models with or without coupling
752 to oceanographic models or ecosystem models (Fiksen and Carlotti, 1998; Carlotti and Wolf, 1998;
753 Zakardjian et al., 2003; Varpe et al., 2007).

754 Descriptions of life cycle components with stage and allometric-linked implications, are rare. This is

despite the importance of the dynamics of egg production, mortality-at-stage variations, etc. This can be seen clearly in the work of Flynn and Irigoien (2009), modelling the potential impact of PUA on copepod nauplii survival from consumption of diatoms.

Another notable oversimplification in zooplankton models which has various important ramifications, is the assumption that the zooplankton C:N:P ratios are constant. Clearly, in copepods that accumulate lipid that is not so. This then affects simulations of nutrient regeneration and also of mortality due to respiration in the absence of food (see above; Acheampong et al., 2012).

5.5. Zooplankton mortality

Zooplankton mortality is the death of individuals and loss of their associated biomass due to predation, starvation, inhospitable environments, or natural death from senescence, genetic malfunction, disease, viral attacks etc. (Carlotti et al., 2000; ICES WKMOR Report, 2010). Whatever the mechanism, mortality is a key process that shapes zooplankton dynamics. Modelling studies have repeatedly illustrated how small changes in mortality translate to large changes in modelled abundance and production (e.g., Steele and Henderson, 1981, 1992, 1995; Twombly, 1994; Ohman and Wood, 1995; Lynch et al., 1998; Speirs et al., 2006; Neuheimer et al., 2009, 2010a,b; Skarđhamar et al., 2011). Further evidence to the importance of mortality is that many aspects of zooplankton migration behaviour (daily and seasonally), life history and reproductive strategies are believed to be adaptations that minimize mortality risk (Kaartvedt, 1996; Ohman et al., 1996; Hays, 2003; Leising et al., 2005c). For example, diel vertical migrations are believed to be a strategy for decreasing visual predation during the day light hours (Cohen and Forward, 2009); likewise, the egg-carrying strategy of cyclopoid copepods has been found to result in lower mortality rates of the eggs compared to suspended eggs spawned by the calanoid copepods (Kiørboe and Sabatini, 1994). During unfavourable periods when food resources are in short supply, many species have developed adaptations such as production of resting eggs or a diapause in late developmental stages. Diapause itself is correlated with an ontongenic vertical migration, which is similar to diel migrations, and decreases visual predation. For the most researched copepod, *C. finmarchicus*, research indicates that in areas with relatively high abundance of potential predators mortality during the overwintering period is much lower than during the

781 growth period of the species during spring and summer (Bagøien et al., 2001; Gislason et al., 2007). The
782 relatively low mortality at depth has been attributed to decreased predator induced mortality risk; the dark
783 habitat provides shelter from visually guided predators, and the non-mobile diapause stages minimize
784 encounters with predators that rely upon mechanoreception (Kaartvedt, 1996; Hirche, 1997; Fiksen and
785 Giske, 1995; Fiksen and Carlotti, 1998; Bagøien et al., 2001). It should be noted, however, that some
786 predator species have adapted to exploit the diapausing zooplankton populations; for example, the North
787 Atlantic right whales have been observed to feed on the diapausing *Calanus finmarchicus* (Baumgartner et
788 al., 2003).

789 **5.5.1. Causes of mortality**

790 **5.5.1.1. Predation**

791 Predation, which includes cannibalism of copepod eggs and nauplii by older copepodites (Ohman and
792 Hirche, 2001; Hirst and Kiørboe, 2002; Ohman et al., 2008; Neuheimer et al., 2009), typically dominates
793 mortality losses (e.g., Hirst et al., 2010; ICES WKMOR Report, 2010), with estimated rates not uncommonly
794 exceeding 100% per day. Predation is arguably the most complicated mortality mechanism to characterize as
795 it depends on the abundance and consumption rates of the predator, both of which are synergistically coupled
796 and influenced by various external (environmental) and internal (fitness) factors. Predator consumption rates
797 depend on the ability of the predator to detect, attack and successfully capture their zooplankton prey which
798 in turn varies with the type, size, age, quality and quantity of the zooplankton as well as other factors, such as
799 the activity of the competing members of the predator guild. All these dependencies are neither simple to
800 measure nor easy to parameterize in models (see below). Predatory losses in the field have been observed to
801 be usually inter-specific: copepods grazing on microzooplankton (Verity and Paffenhöfer, 1996), fish
802 feeding on copepod eggs (Mauchline, 1998), various chaetognath and krill species feeding on copepods
803 (Ohman, 1986; Båmstedt and Karlsson, 1998; Tönnesson and Tiselius, 2005; Bonnet et al., 2010), jellyfish
804 preying on zooplankton and fish (Mackie et al., 1987; Purcell and Arai, 2001).

805 Cannibalism within a species has also been noted in both micro- and mesozooplankton occuring
806 even in the presence of abundant potential prey alternatives. For example, in laboratory experiments, the

microzooplankter *Oxyrrhis marina* has been found to demonstrate cannibalism whilst rejecting the phytoplankton *Isochrysis galbana* due to its poor quality (Flynn et al., 1996), while the adult copepod *Sinocalanus tenellus* has been found to cannibalise on its naupliar stages despite the presence of other palatable prey items (Hada and Uye, 1991). Ohman and Hirche (2001) found that egg mortality in the copepod species *Calanus finmarchicus* was directly related to the abundance of females in the population and concluded that this may be a self-regulating mechanism. However, *Temora longicornis* (copepod) have been reported to cannibalise on their naupliar stages only when alternative (algal) prey items are limiting (Daan et al., 1988). In some instances cannibalism has been found to occur simply as a reflection of high concentrations of the predator, as exhibited by the dinoflagellate *Protoperidium* spp. (Jeong and Latz, 1994). Such intraguild predation may occur when the maximum carrying capacity of the ecosystem has been reached.

Predation of zooplankton is the process by which nutrients and energy are transferred to the higher trophic levels. Therefore, accurate estimates of copepod mortality rates are essential for understanding zooplankton ecology, trophic links, ecosystem dynamics, and for predicting ecological responses to climate-related changes in the environment.

5.5.1.2. Non-predatory losses

Non-predatory losses can also be significant, accounting for as much as one third of copepod mortality globally (Hirst and Kiørboe, 2002). Starvation may be more important for smaller zooplankton that have limited ability to store reserves (e.g., copepod nauplii vs. copepodites; Elliot and Tang, 2011; Tsuda, 1994). Copepod egg mortality, also referred to as non-viability or non-hatching of eggs, is regularly on the order of 10-20% (Irigoien et al., 2002) but can sometimes be as high as 90% (Miralto et al., 1999). This is typically attributed to effects of poor female diet or condition (Jónasdóttir et al., 2009). Starvation is not relevant for non-feeding stages (e.g., *Calanus* N1-N2 and males). However, the first feeding stage (N3) and the first copepodite stage C1 are critical points in ontogeny (Peterson, 2001); and higher mortality for these critical stages has been observed (Eiane and Ohman, 2004). Lack of food or poor food quality can often affect ontogenetic growth and development (Koski et al., 1998) leading to higher mortality risk. To what

833 extent these fatalities are due to bacterial or fungal infections, inborn errors in metabolism, intrinsic
834 biochemical failures, or the lack of adequate food is not clear.

835 **5.5.1.3. Mortality due to environmental factors**

836 Environmental influences on mortality can be complicated and far-reaching. They indirectly affect
837 through their influence on predator guild size and composition, and behavioural factors related to predator
838 consumption (e.g., predator and prey condition, prey motility, etc.). Higher water temperatures often
839 correlate with increased mortality rates (Hirst and Kiørboe, 2002; Plourde et al., 2009); this may be a causal
840 relationship (i.e., temperature tolerance is exceeded; we do not know what the upper limits are for most
841 species). However, it is more generally believed that temperature serves as a proxy for other processes.
842 Higher temperatures can cause a myriad of problems, including increased disease and parasitism (Harvell et
843 al., 2002), starvation risk (Tsuda, 1994), hypoxic conditions (Stalder and Marcus, 1997; Tiselius et al.,
844 2008), decreased life span or changes in predator abundance and predation rate (Myers and Runge, 1983).

845 **5.5.2. Estimating zooplankton mortality in the field and laboratory**

846 **5.5.2.1. Field estimates**

847 Field estimates of zooplankton mortality are usually derived from observational data for zooplankton
848 abundances and additional information about their population dynamics, such as reproduction and
849 developmental rates. Most estimation methods are formulae that are based on an underlying model of
850 zooplankton population dynamics, and therefore it is somewhat difficult to separate field studies from
851 modelling studies. Furthermore, various errors associated with mortality estimation methods could arise due
852 to (i) uncertainty in the values of input variables used in the formula and/or (ii) violations of the assumptions
853 used to derive the formula. It is thus necessary to take into account both these issues in order to avoid
854 introduction of unknown bias into the mortality estimates, or application of formulae that are inappropriate.
855 In a comprehensive analyses using theoretical studies, field data, and individual-based population dynamics
856 modelling, Gentleman et al. (2012) examined the importance of these issues for estimating the mortality of

the different stages of the copepod identifying the limitations of the existing methods and making recommendations on how best to increase accuracy in the estimation of mortality rates.

Gentleman et al. (2012) found that the sampling protocol, choice of method and data used for the mortality rate estimation can have a pronounced effect on the resulting estimate; which is the best method to employ depends on the situation. For example, they demonstrated that stage ratios in copepods varies even over a short period thus challenging the typical belief of relatively stable stage ratios and stressing the importance of high resolution stage-demography. This is important in order to provide realistic confidence intervals for estimates (e.g., Bi et al., 2011) as pooling data from different regions, time intervals and/or across life stages (such as is necessary when there are missing stages in the data) is likely to be inappropriate and limit mortality estimates due to differences in the population stage structure. They concluded that there is a need to work towards development of new methods that are less restrictive and which could make use of dynamic simulations, for example, to identify potential temperature and food variability as well as advective sources and losses.

5.5.2.2. Laboratory estimates

Field studies are based on observations of the survivors, and therefore, estimate losses due to multiple mortality mechanisms, as well as (often unintentionally) other losses including sinking, advection etc.. In contrast, laboratory studies are generally directed as quantifying mortality due to a single mechanism, typically predation by one predator species on one prey type. These experiments typically use a limited number of predators exposed to a restricted type of prey, and measure loss rates after a set period of time (Sell et al., 2001). Mortality is typically reported as a predator clearance rate; i.e., fraction of the prey population consumed per capita predator. Thus, in theory, laboratory studies provide a measure of predation losses when the size of the prey and predator populations in the field is known. The issue with such studies of course is that they have limited variability, and cannot usually account for any behavioural changes in the predator which could occur in the presence of mixtures of prey types, variable environmental conditions and/or competing predator species. Moreover, the laboratory estimates only typically account for predation,

and not other mortality mechanisms (e.g., starvation). Thus it may not be appropriate to simply scale up laboratory measurements of predation to estimate field mortality.

In conclusion, it can be difficult to get realistic mortality estimates from field, laboratory or mesocosm studies; it is thus essential to use all the available approaches, field and laboratory based, in conjunction with modelling.

5.5.3. Modelling studies of zooplankton mortality

It is generally acknowledged that mortality rates are the most uncertain parameter in models, and as such, it is common practice to either (i) assign some particular value and perform the simulation, potentially including post-hoc sensitivity analyses, or (ii) use observational data to constrain model abundances and biomass, and tune the mortality-related parameters such that the model results reasonably match the data. The latter practice is a form of parameter estimation (also called inverse modelling, data assimilation), which can either be done by trial and error or by a more automated approach using sophisticated modelling techniques (e.g., effectively creating a “shooting method” solution to the boundary value problem) that sometimes are designed to measure uncertainty (e.g., Monte-Carlo methods or genetic optimization algorithms).

Typically, intrinsic mortality (i.e., non-predatory losses, death due to environmental factors) within ecosystem models, is if described at all, applied at set rates at different age stages (e.g., Flynn and Irigoien, 2009). Modelling of predation on zooplankton is similar in scope, and thus in limitations, to approaches used to describe zooplankton predation on lower trophic levels. It is rare that the fate or activity of specific groups are modelled. More often whole groups, if not all zooplankton, are merged into what could be viewed as a closure term on the phytoplankton and bacteria (in biogeochemical models). By the same token, predation on zooplankton *per se* is not often modelled, rather a closure term is applied; closure implies some kind of functional response of the predators coupled with an assumed time-variation of the predators.

In ecosystems models where zooplankton mortality is explicitly considered, it is often represented as a loss term to zooplankton variables, Z, that represent the biomass or abundance of a particular group (e.g.,

age, stage, size-class of a population, or community/functional type), or as a probabilistic risk of death for individual-based population dynamics models. There is a disconnect between how models characterize these loss terms/risks and the zooplankton mortality mechanisms outlined above (Section 5.5. Introduction) mainly due to the challenges of characterizing predation-related mortality. It is impractical if not impossible for models to explicitly account for all the factors affecting zooplankton mortality. To do so would require realistic simulation of the dynamics of all higher predators in the predator guild as well as quantifying numerous dependencies and behaviours of both prey and predator and for which the functional relationships are generally unknown; in addition to quantifying all non-predation mortality mechanisms. Thus, representation of mortality in models is always a simplification, and is therefore always a source of uncertainty.

The choice of mathematical form for the mortality loss/risk term depends to some extent on the model structure. For models that explicitly include higher predator abundances, either as dynamic variables or forcings, predation mortality is described as the product of predator abundance and predator functional response using analogous formulations for zooplankton grazing. However, most zooplankton models (both population and lower trophic ecosystem) do not explicitly account for higher predators, and so must proxy the effects of predation along with other mortality mechanisms as part of the closure term. For models using differential equations, closure is usually characterized by an instantaneous loss rate that varies with Z, according to linear, quadratic, hyperbolic or sigmoidal relationships (Fig. 6). The linear and quadratic variations are the two most common formulations and can be construed as predation mortality for a constant-biomass predator exhibiting non-satiating Type 1 vs. Type 3 functional response (Gentleman and Neuheimer, 2008). The quadratic formulation can also be argued to represent cannibalism or intraguild predation, for which the predator biomass that is proportional to Z, and the predators, exhibit a non-satiating Type 1 functional response. For models using differential equations, the mortality loss over the time step is typically defined by assuming a linear closure with constant mortality coefficient, such that survivorship at the end of the model time step is given by: $Z(t+\Delta t) = Z(t)e^{-\mu\Delta t}$ (where, Δt denotes change in time and μ is the rate of loss). For individual based models, the probability of survival (1 – probability of dying) during the interval [t, t+Δt] is similarly based on a constant mortality described as: $P_{survive} = e^{-\mu\Delta t}$ (Gentleman et al., 2012).

There are a number of issues related to the above approaches to modelling mortality. First, the choice of closure scheme is generally based on theoretical arguments rather than specific mechanisms or observations. Thus, the closure term typically lumps all the processes leading to mortality (internal and external) into a single process (akin to that in NPZBD); the interactions between mortality and other physiological processes as well s feedback mechanisms of these vital rates on mortality rates (Fig. 2), innate to biological systems, are ignored. However, there are dozens of studies demonstrating how this unsupported choice has a pronounced effect on trophic dynamics and ecological stability (e.g., Steele and Henderson, 1981, 1992; Edwards and Yool, 2000; Fulton et al., 2003). Choice of value for the coefficients in any particular closure scheme can have similar effects on ecological stability (e.g., Neubert et al., 2004), yet parameter values are almost always borrowed from previous modelling studies without any observation support of these values (Plagányi, 2007). Moreover the influences of environmental factors (e.g., temperature, food etc.) on mortality-related coefficients vary among modelling studies. Many ignore variation, and those that do consider environmental dependencies are typically limited to temperature, choosing to apply a similar Q10 to what is applied to all other rates, despite evidence to the contrary. However, it would be vastly erroneous to use Q10 values for mortality that are similar to Q10 for growth or development as field estimates of Q10 for mortality have been observed to be significantly greater than for growth/development (e.g., Q10 growth/development Calanus=2-3 vs. Q10 mortality=8; Plourde et al, 2009). Another issue relates to the necessity of partitioning the total mortality loss into different components (e.g., natural death vs. predation), which itself is often done with an arbitrary parameter; despite this partitioning being critical for estimating the proportion of secondary production that is passed to trophic levels vs. that which is designated to detrital pools that sink from the surface waters (i.e. contributes to export production).

What these models do demonstrate though, similar to the zooplankton feeding models, is that the incorporation of even biologically simplistic formulations of mortality have the potential to destabilize the system or predict very different population dynamics. However, based on the very significant flow of energy and materials within the zooplankton component itself (Fig. 1; Table 1), one may question the validity of using these closure terms. The activity within the zooplanktonic community is so great that it may be more prudent to replace the traditional closure term applied to the zooplankton compartment, intended in large

961 measure to summarise the top-down control levied by the higher trophic levels, with an intraguild
962 cannibalism term (Mitra, 2009).

963 **5.6. External forcings: temperature, pH, turbulence and seasonality and patchiness**

964 **5.6.1. Temperature**

965 Temperature is probably one of the major external forces affecting physiological processes of marine
966 organisms and is a limiting factor in zooplankton growth dynamics. Typically the rate of biological change is
967 expressed over 10°C temperature difference, $Q_{10,}$ where a Q_{10} of ca. 2-3 is usually applicable for most
968 biological systems. Q_{10} does vary between organisms, and can also differ between physiological functions of
969 the same organism.

970 **5.6.1.1. Field and experimental studies of temperature**

971 Impacts of temperature on zooplankton growth and respiration rates are relatively well studied
972 (Ikeda et al., 2001; Hernandez-Leon and Ikeda 2005; Castellani et al., 2005b; Castellani and Altunbaş, 2013)
973 although the physiological mechanisms through which temperature affect metabolism may not always be
974 clear (Clarke and Fraser, 2004). Temperature affects all phases of zooplankton growth and life cycle; for
975 example, feeding (Møller et al., 2012) and reproduction (Holste et al., 2008; Kjellerup et al., 2012) vary
976 between and within species as well as biogeographic location. Increase in temperature typically implies an
977 increase in the physiological processes reaching a maximum limit beyond which the zooplankton systems
978 become damaged (e.g., respiration; Fenchel, 2005; Hernández-León and Ikeda, 2005). Increasing
979 environmental temperatures induce decreasing body size due to differential responses of development rate
980 versus somatic growth, resulting in different potential reproductive output (Halsband and Hirche, 2001;
981 Arendt et al., 2005; Jónasdóttir et al., 2005). Conspecifics tend to be smaller in warmer locations (Deevey,
982 1960) with shorter generation times and lower per capita reproduction rates, but in compensation produce
983 more generations per year (Halsband-Lenk et al., 2002).

984 It has been suggested that a zooplankton species may acclimatise to varying seasonal temperatures
985 (Carlotti et al., 2000) by altering their ingestion rates (Thébault, 1985; Saiz and Calbet, 2007; Møller et al.,

2012), gut clearance rates (Dam and Peterson, 1988), and/or basal as well as metabolic respiration rates. Zooplankton metabolic rates typically show an exponential increase with temperature with Q_{10} of ca. 2-3. However, a recent study by Castellani and Altunbaş, (2013) reported that the seasonal changes in the acclimatised respiration rate of the copepod *T. longicornis* with *in situ* temperature was described by a sigmoid trend with Q_{10} ranging from 1 to 2.88 and they attributed such variation to copepod nutritional and reproductive state. Saborowski et al. (2002) investigated temperature effects on respiration rates in the krill *Meganyctiphanes norvegica* from three geographically separate populations; Kattegat, the Clyde Sea and the Ligurian Sea. These three populations experienced differences in spatio-temporal temperature variation, together with differences in trophic conditions. It was found that the respiration rates among these three different populations were similar when incubated at their respective ambient temperature conditions (9°C, 5°C and 12°C for Kattegat, the Clyde Sea and the Ligurian Sea, respectively). This suggests that krill are able to adjust their metabolic rate to the prevailing thermal conditions. On the other hand, certain vital rates seem to require specific temperatures, irrespective of location and temperature regime. For example, temperature responses of the female *Centropages typicus* for survival, embryonic and post-embryonic development vary between populations in the boreal North Sea and the sub-tropical Mediterranean, while the optimum temperature for egg production is the same in both regions and also in different seasons within the same region (Halsband-Lenk et al., 2002).

Ecologist and physiologists have long been interested in the way zooplankton metabolism (usually measured as oxygen uptake) reacts to the changing of the seasons and to the varying of ecological conditions at different latitudes (Cossins and Bowler, 1987). In particular numerous studies have looked at the effect of temperature by comparing the Metabolism-Temperature curve (i.e., M-T curve) of zooplankton for different seasons (Gaudy and Thibault-Botha, 2007) or from different latitudes (Ikeda, 1985). However, in the field zooplankton metabolism is also affected by changes in body size, food availability/quality, activity, growth and reproduction and, therefore, seasonal and latitudinal fluctuations in respiration should not be interpreted simply as the effect of temperature (Clarke, 1993).

From the perspective of zooplankton communities, it has been argued that the effect of temperature on the growth of the total community *per se* may be negligible or even zero (Hirst and Lampitt, 1998); while

specific species are adapted to live under specific temperature regimes, different species will dominate under different temperature conditions. Thus the specific populations may fluctuate, however, the community as a whole would not undergo any significant changes. It has been proposed that the succession of zooplankton may be dependent on the variations in the temperature (Adrian and Deneke, 1996; Calbet et al., 2001). All this continuing effort on zooplankton temperature-related physiology contrasts with that on temperature relationships for phytoplankton, which typically refer back to classic papers such as Eppley (1972), or to the recent modification thereof (Bissinger et al., 2008). In consequence, the information about the impacts of subtle changes in temperature on zooplankton is probably more complete than that for their phytoplanktonic prey.

5.6.1.2. Modelling descriptions involving temperature

In modelling studies the impact of temperature on zooplankton is typically described through the usage of an averaged Q_{10} value. However, it has been argued that the impact of temperature would vary for the different physiological functions (Carlotti and Poggiale, 2010) and also for the different developmental stages (Campbell et al., 2001); indeed some (very few) models do incorporate a non-linear function describing the relationship between zooplankton physiology and temperature (Travers et al., 2007). Moreover, Q_{10} values may only apply for part of the range actually experienced by the organisms (Møller at al. 2012). Existing stoichiometric models of zooplankton could be configured to consider the effects of temperature on these processes. For example, within the model of Mitra and Flynn (2007), the maximum growth rate and respiration rates could be described as functions of temperature. However, as the different zooplankton physiological processes may not vary pro rata with alterations in the temperature, but show significant differences in the rates of changes, such an inclusion may not be simple.

Various empirical models, specifically focussed on copepods, have been proposed to describe the relationships between temperature, development and growth (see Hirst and Lampitt, 1998 and references therein) as well as temperature and mortality (see Hirst and Kiørboe, 2002 and references therein). Embryonic and post-embryonic development generally is described with the Bělehrádek empirical equation that varies with the local temperature regime (McLaren, 1965, Table 47 in Mauchline, 1998) although it has

been shown that this function is not drastically different from using a Q_{10} value (Gentleman et al., 2008). Vital rate descriptors incorporating Q_{10} or Bělehrádek's equation do not include a maximum temperature beyond which metabolic activities will stop (so the vital rates increase with increases in temperature). An additional concern is that egg production rates are often modelled using Q_{10} or Bělehrádek descriptors even when there is no clear evidence of temperature dependency, or when such dependency is observed, the relationships do not translate from one region to another for the same species (Gentleman pers obs).

Given that most zooplankton models in ecosystems describe whole Z communities, the Hirst and Lampitt (1998) view (see above) may be quite acceptable, that there is no significant impact of temperature. However, it is more difficult to accept such an argument in end-to-end models where specific fish are dependent on specific zooplankton, both/all of which will certainly respond differentially to temperature.

5.6.2. pH

Since the beginning of the industrialisation in ca. 1750, the CO_2 content in the atmosphere has increased from 280 ppm to 380 ppm (Feely et al., 2004). Today approximately 6.5 Gt a^{-1} C is released into the atmosphere by the burning of fossil fuels (IPCC, 2007). The oceans absorb ca. 2.2 Gt a^{-1} C in form of CO_2. This surplus of CO_2 decreases the pH of seawater. This effect is known as ocean acidification (OA; Royal Society London, 2005). Under decreased pH conditions, the solubility of calcium and its derivatives increases threatening organisms that contain calcite or aragonite.

5.6.2.1. Field and experimental studies of pH

In the pelagic zone, the most endangered zooplankton species appear to be the thecosomatic pteropods. Pteropods are holoplanktonic zooplankton organisms which mainly live in the open ocean (Bé and Gilmer, 1977). Some groups of them build an aragonite shell. Experimental evidence has shown that the shells of these organisms are damaged under high CO_2 concentrations (Orr et al., 2005) and that physiological activities are enhanced to cope with such high CO_2 concentrations (Maas et al., 2012).

Zhang et al. (2011) have shown through a comparative study on toxicity of OA on several marine copepods that benthic copepods are more resilient than pelagic and that herbivores such as *Calanus sinicus*

are more tolerant than omnivorous and carnivorous copepods. Low pH has been found to induce reproductive failure due to a decline in egg hatching success (Mayor et al., 2007; Kurihara and Ishimatsu, 2008). It has been suggested that zooplankton, such as jellyfish, may benefit from acidified conditions when competing with other, more sensitive species (Atrill et al., 2007). The impact of pH on the aquatic community and thence zooplankton is a new area of research; thus there are insufficient data (from observations and experiments) to enable validating of such hypotheses (Richardson and Gibbons, 2008).

5.6.2.1. Modelling descriptions involving pH

While pH is increasingly included as a parameter in models of marine ecosystems (e.g., Artioli et al., 2012), models specifically relating changes in plankton physiology with pH are rare. Physiologically, the critical issue is not the pH of the bulk water (which is the parameter value reported in ecosystem models, and that typically measured in experimental studies), but of the water immediately surrounding the organism. In a recent modelling study, Flynn et al. (2012) show for plankton how the acidity (i.e., $[H^+]$) next to the organism varies with particle size and metabolic activity, and also with the initial bulk water $[H^+]$. The larger and more active the zooplankton the greater the $[H^+]$ increase over the bulk water values (i.e., large active organisms experience more extreme OA conditions). However, the consequences are likely mitigated by large animals having lower surface area to volume ratios so that external conditions have less leverage on internal homeostasis. Also, these zooplankton will have evolved to survive a more variable external $[H^+]$. The real issue is that with OA the buffering capacity of the water decreases so that deviations in $[H^+]$ become larger for a given level of metabolic activity. As algal blooms (temporarily) raise local pH, clearly there is scope for differential impacts of OA on zooplankton of different size, activity and skeletal structure under different trophic interactions.

Aside from the effects of global change on pH, the consequences of natural increases of pH during dense phytoplankton blooms, promoted in many occasions by human activities (notably eutrophication), are seldom considered. In this regard, it has been suggested that high pH could actually be detrimental for many dinoflagellates and ciliates (Pedersen and Hansen, 2003a,b; Hansen et al., 2007).

5.6.3. Turbulence

5.6.3.1. Field and experimental studies of turbulence

The likelihood of the predator encountering food or prey is a function of the water turbulence, irrespective of the quality and quantity of food available. While a low level of turbulence may increase the likelihood of encountering prey, a higher level of turbulence would be detrimental to the predator (Saiz et al., 1992; Havskum, 2003; Metcalfe et al., 2004). Turbulence may also set physical limits on the ability of copepods to be at a preferred depth, and hence may explain the presence of nauplii in areas with low levels of turbulence (Maar et al., 2003) that would then impact upon transport, growth opportunities and thence trophic dynamics. The thresholds at which turbulence has effects on plankton are highly species specific, and respond to the feeding mechanisms involved in capture of prey. For instance, the feeding rates of the ambush copepods *Oithona davisae* appeared to be much more impaired by turbulence than other species (Saiz et al., 2003). This result agrees with field observations of *Oithona* sp. occurring deep in the water column under episodes of high surface turbulence (Incze et al., 2001; Visser et al., 2001). Regarding protozoans, experiments with the ciliate *Strombidium sulcatum* suggest a negative effect of turbulence on growth and grazing rates. Conversely, *O. marina* decreased their size under turbulence, but increased their growth rates (Saiz et al., 2003), although Havskum (2003) found the effects of turbulence on this species were highly dependent on the turbulent intensity applied. Other dinoflagellates are more sensitive to turbulence, such as the case of *Pfiesteria piscicida* (Stoecker et al., 2006), and the primarily phototrophic *Ceratium tripos* (Havskum et al., 2005).

5.6.3.2. Modelling descriptions involving turbulence

There are various mathematical models exploring how turbulence impacts the potential of the zooplanktonic predator encountering another predator or a prey item (Evans, 1989; Kiørboe and Saiz, 1995). These models focus on the physical aspects of predator-prey dynamics. Caparroy and Carlotti (1996) proposed an individual based model simulating the impacts of micro-scale turbulence on the physiological processes of the copepod *Acartia tonsa*. This was achieved by formulating ingestion to be a function of turbulence. Such an approach can be easily built into mechanistic stoichiometric models describing

zooplankton population dynamics for use within end-to-end ecosystem models at the point of ingestion. Additionally the description of respiration rates would also need to be modified to take in to account of environmental conditions on changes in respiration rates. For example, it has been observed that increase in suspended sediments in the water column are negatively correlated with egg production rates in *Temora longicornis* suggesting that sediment interferes with its feeding rate (Castellani and Altunbas, 2006). Such a decrease in the egg production rate may be not just due to lower efficiency in the ingestion rate but instead a function of the high sediment load leading to an increase in energy (i.e., high respiration rates) diverted by the copepod to searching for food sources or sorting food from sediments, rather than reproduction.

6. Concluding discussion

Our primary aim in undertaking this review was to integrate disparate information about the physiology and functionality of the zooplankton community and to identify gaps between the two research practices (and thence philosophies) of experimentation and modelling. In attempting to do so, we have come across various hurdles, not only between the two research strands but also within each research strand. Table 2 gives an overview of the current coverage of the topic in the literature. From this it is very apparent that large gaps exist in some groups in comparison with others, but that even for the best studied groups the extent of the knowledge base, and our modelling of it, is patchy. When one considers the importance of the description of zooplankton in even simple models (Fig. 3), the need to meet the challenges becomes all the more clear. We summarize these gaps below considering generic issues associated with zooplankton predator-prey status, and then according to the specific issues relating to micro- and then meso-zooplankton communities. Finally we bring these issues together for considerations of challenges associated with modelling.

6.1. Prey status (quality plus quantity) and predator biomass

The importance of experiments in which the implications of prey (nutritional) quality as well quantity are studied needs to be recognised. Indeed prey quality should not be defined according to just differences in taxonomy but also according to the biochemical composition of the individual. This is especially important for phytoplanktonic prey where the nutrient ratio varies widely over the life cycle

depending on nutrient availability with lack of nutrients typically resulting in the accumulation of secondary metabolites (toxins) within phytoplankton (Granéli et al., 1998). This in turn could result in predator avoidance of these prey types which would then form (harmful) algal blooms (Colin and Dam, 2003; Mitra and Flynn, 2006a). Very few experimental studies (e.g., Flynn and Davidson, 1993; Koski et al., 1998; Plath and Boersma, 2001; Jones and Flynn, 2005) have considered the effect of changes in elemental composition (either C:N or C:P) within a prey item on zooplankton population dynamics. And there are none which look at the changes in the elemental composition in entirety (e.g., C:N:P:fatty acids etc. of prey and the zooplankton predator).

An additional problem associated with measuring phytoplanktonic prey biomass is that this is often measured in terms of chlorophyll and a crude conversion is used for derivation of the carbon biomass of the phytoplankton (e.g., Moloney and Gibbons, 1996). To improve the value of future phytoplankton-zooplankton experimental studies it is important not to use chlorophyll as the unit for phytoplankton biomass, because of the variability in chl:C with nutrient status and irradiance (Kruskopf and Flynn, 2006). However, data for C-biomass supported by C:N:P (:fatty acid etc.), are missing from most studies. Conversions from proxies such as length or diameter are better than nothing but they are no real substitute for data from elemental analysis, etc.

6.2. Microzooplankton studies – strict heterotrophs vs. mixotrophs

Throughout the work that is summarised in this paper, a group of organisms was consistently under, or misrepresented; these are the mixotrophic protists. The term microzooplankton is typically used to imply strictly heterotrophic protists and thus ignores what are increasingly recognised as ecologically important components of this community – the mixotrophs (Flynn et al., 2013). Studies on mixotrophs tend to be sidelined as a subject-area in itself rather than integrated as part of the microzooplankton community. The ability to photosynthesize, through acquired phototrophy, in organisms such as ciliates (Stoecker et al., 2009) provides an important additional nutritional route in addition to phagotrophy. That these processes occur within a single cell is a process which adds yet another degree of complexity to the already complex and generally poorly understood physiology of microzooplankton. It is, nonetheless, an important topic that

needs attention so that we may better understand the implications of phagotrophy ***plus*** phototrophy within the community as well on the lower and upper trophic levels.

6.3. Mesozooplankton studies – "copepod-heavy"

Copepods are typically considered as the representative of the mesozooplankton community. This is evident from the various national and international research programmes which have focussed on copepods, the availability of abundant experimental data and indeed the presence of ample copepod-focussed models (See also Table 2). While copepods undoubtedly do play an important role in the food-web interactions globally, equally important are other members of the mesozooplankton community such as krill, jellyfish, chaetognaths and the larval stages of fish.

While mesozooplankton studies typically focus on copepods, often these only focus on the adult female. There is a need for parametric information on the activity of the entire life cycle rather than on just one event in a particular life stage (e.g., egg production) (Campbell et al., 2001). Not only will the prey items vary for different life stages, but ingestion rates and assimilation efficiencies and thence growth rates and loss processes would also be expected to be markedly different.

6.4. Modelling challenges

If one was to argue that our ability to model zooplankton should give an indication of our understanding of the real organisms then we could conclude that we know frighteningly little with any surety. In reality, we know much, but we lack holistic integration of that knowledge in models due to the old issues of data (in)adequacy and model complexity. Those excuses aside, there are clear opportunities for relatively easy improvements in zooplankton models. Below we highlight some key areas for investigation.

1. Food selectivity: Even simple models usually contain some level of food selectivity, but field workers, including those investigating long-term changes in plankton succession, often identify detailed links between prey and predator species composition and the production cycle. It would help to have information especially concerning the consumption of phototrophs such as diatoms and coccolithophorids, versus consumption of mixotrophs (the latter have more constrained

stoichiometry, and are often classed within the microzooplankton). Food selectivity affects ingested food quality. These interactions may be considered between plankton functional types (e.g., diatoms vs. mixotroph consumption; effects of climate change, ocean acidification), and within types (e.g., impacts of nutrient status, which may be affected by climate change impacts on water column stability). Food selectivity affects the operational value of G_{max}, a parameter of key importance (Fig.3) and usually set as a constant (Fasham et al., 1990; Gentleman et al., 2003), but which in the context of responding to quality and quantity is not constant (Mitra and Flynn, 2007). We need to be able to better describe these interactions. For this we need more extensive knowledge on what the different zooplankton functional types eat in the field, and how they select prey especially in environments where a wide range of prey are available; i.e., we need more experimental studies of mixed diets which, in addition to zooplankton vital rates, record changes in prey physiology (e.g., C:N:P status) over time.

2. Kinetics of prey consumption and growth: While simple models relate zooplankton growth to prey availability using a rectangular hyperbolic function and fixed assimilation efficiencies (assimilation efficiency), there is more than ample evidence to show a biphasic interaction, complicated by feedback from satiation to ingestion, and from satiation to throughput and hence to variable assimilation efficiency. The implied density-dependant inefficiency (Mitra and Flynn, 2007; Flynn, 2009), perhaps with sloppy feeding (Møller et al., 2003), has important implications for system dynamics (Flynn, 2009), which urgently need to be established or refuted. Both G_{max} and assimilation efficiency are known to be critical parameters affecting models of trophic dynamics (Fig.3).

3. Form of voided excess ingested material: The fate of excess ingested material has important implications for system dynamics. If excess C is “burnt off” through respiration then there is a direct and rapid concurrent regeneration of inorganic N and P to support primary production. Release of DOM would support bacteria, and thence microzooplankton and mixotrophic production. Release of POM as rapidly sinking pellets, however, supports production below the ergocline, in a very different system.

4. Sensitivity of mortality at different age-stages to prior nutrient history: It is clear that different mortality rates at different stages of mesozooplankton life histories have potential for important implications on trophic dynamics. This is seen in the studies of the effects of polyunsaturated aldehydes upon nauplii stages of copepods on consumption of diatoms by the adults (Miralto et al., 1999; Flynn and Irigoien, 2009). Aside from that specific example, mortality in juveniles is likely to be a combination of inborn errors in metabolism, together with nutritional issues related to the health of the egg-laying adults and food availability (quality and quantity) for the early stages. This component of the system dynamics warrants investigation so as to enable its consideration in modelling.

5. Steady state versus dynamic studies: For verification of models used in ecosystem scenarios, dynamic time series data are required; steady state data are of little relevance in studies of dynamic ecological processes not least because of the importance of nutrient history. It is of vital importance to have complete datasets for the different components (predator, prey, nutrients) of the total system.

It is noteworthy that in the much-cited work of Follows et al. (2007), trait selection in the description of the planktonic food web was developed entirely within the phytoplankton; there were many dozens of phytoplankton grazed by two zooplankton types (each of which had simple structures). Given that prey selection, and grazing resistance can have such powerful affects on succession, easily overriding bottom-up autecology traits, one may wonder how the results of that study may have developed if the traits of the zooplankton models had been accorded the same level of investigation as had the phytoplankton. To do that would have required the type of extensive consideration of model development that phytoplankton have received over the last decade (Allen and Polimene, 2011).

The time has come for zooplankton models to rise in their status within marine biogeochemical and fisheries models. We have shown that the behaviour of the zooplankton model is pivotal, and that various empirical studies are required to enhance our understanding so that models can be better constructed and tested. Studies of biological and ecological systems should ideally be conducted according to the iterative process of observation, experimentation, modelling etc. Now is the time to go forward with the next cycle of

1245 the experiment-model-observation loop. The research conducted within the EuroBASIN project will help to
1246 achieve that goal. Once we have been through that process we will be better placed to decide on the optimal
1247 balance of model complexity and fidelity. Until that time, we must remain aware that ultimately models are
1248 only as good as the behaviour (performance) of the weakest submodel, and that zooplankton models are
1249 currently anything but as well founded as models are of the phytoplankton, or indeed of fish.

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1945 **Table 1:** Classification of zooplankton according to their physiological functionality.

Zooplankton Type	Physiological functionality
Protist: (microzooplankton)	Single-celled organism without a gut, with relatively simple and rapid life cycle strategies (e.g., reproduction through binary fission with generation times typically 0.5-few days). Digestion period can equate to a large proportion of the life cycle. Potential for high efficiency for retention of ingested N and P especially in mixotrophic forms.
Non-mixotrophs	Purely heterotrophic protists (i.e., capable of only capturing food); e.g., *Oxyrrhis*, *Paraphysomonas*.
Mixotrophs	Protists that possess the capability to fix carbon (photosynthesis) as well as capture food (phagotrophy); e.g., plastidic ciliates.
Non-protists: (mesozooplankton)	Multicellular organisms typically with a gut, with relatively complex life cycle strategies (e.g., age structured populations).
Crustaceans	Often display swarming behavioural traits. Often maintain energy (oil) reserves; e.g., copepods, krill, cladocerans; some benthic forms release pelagic larvae (e.g., Nauplius, Zoea). Life cycle extending far beyond planktonic stages in larger crustaceans.
Non-crustaceans:	
Cnidaria	Meroplankton and holoplankton encompassing a wide variety of sizes and life-cycle strategies (e.g., polyp, medusa, colonial siphonophores); may display swarming behavioural traits, due to asexual and sexual reproduction. Variable allometry in predation; most physiological studies focus on a few meroplankton species (e.g., *Aurelia* spp.); e.g., cnidarian jellyfish.

Ctenophore	Holoplankton, similar to Cnidarians but without stinging nematocysts; no gut per se; most physiological studies focus on a few species (e.g., *Mnemiopsis* and *Pleurobrachia* species); ctenophore jellyfish, commonly referred to as "comb jellies".
Polychaetes	Meroplankton (Trochophora and Nectochaeta larvae), some holoplanktonic forms (e.g., Tomopteridae); carnivorous
Pteropodes	Holoplanktonic; mainly oceanic; Thecosomata (shelled) feed on phytoplankton and seston, threatened by ocean acidification; Gymnosomata (unshelled) are carnivorous
Chaetognaths	Mainly planktonic; carnivorous (including cannibalism); exclusively marine; e,g., *Sagitta*, *Eukhronia*.
Tunicates	Planktonic forms considered here; all are planktivores; with gut; wide (non-allometric) feeding range; e.g., salps, doliolids, appendicularia.
other meroplankton	Different larvae of benthic organisms (e.g., echinoderm larvae)
Larval fish	Like crustaceans but with life cycle extending far beyond the planktonic phase (i.e., similar to larger crustaceans).

Table 2: Summary of empirical understanding and modelling activity for different zooplankton types. Good status ●, limited status ◒, minimal status ○. Data collated from field (F), laboratory (L) and modelling (M) studies.

	mixotroph			heterotrophic µzooplankton			copepod			krill			jellies			tunicate			chaetognath			pteropod			fish larvae		
	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M	F	L	M
prey detection & selection	◒	◒	◒	◒	◒	◒	●	●	◒	●	◒	○	●	●	○	◒	◒	◒	●	○	○	●	○	○	◒	◒	◒
prey capture	●	●	◒	●	●	◒	●	●	◒	◒	◒	○	◒	◒	○	◒	◒	◒	●	○	○	●	○	○	◒	◒	◒
ingestion rate with prey quality	○	○	○	○	◒	◒	◒	●	◒	○	◒	○	◒	◒	◒	○	◒	◒	◒	○	○	◒	○	○	◒	◒	◒
ingestion rate with prey quantity	◒	◒	◒	◒	◒	◒	◒	●	◒	◒	◒	◒	◒	◒	◒	◒	◒	◒	◒	○	○	◒	○	○	◒	◒	◒
gut transit time & digestion	○	○	○	○	◒	○	◒	●	◒	◒	◒	◒	◒	○	◒	◒	◒	○	●	○	○	○	○	○	◒	◒	◒
assimilation	○	○	◒	○	◒	◒	◒	◒	◒	◒	◒	◒	○	○	○	◒	◒	○	○	○	○	○	○	○	◒	◒	◒
vioding	○	○	◒	○	○	◒	◒	◒	◒	◒	◒	◒	○	●	○	◒	●	○	●	○	○	◒	○	○	◒	◒	◒
stoichiometry	○	○	◒	○	○	◒	◒	◒	◒	◒	◒	○	◒	●	◒	◒	○	○	◒	○	○	◒	○	○	◒	◒	◒
respiration	○	◒	◒	○	◒	◒	◒	●	◒	◒	◒	◒	○	◒	◒	○	○	○	○	○	○	○	○	○	◒	◒	◒
regeneration	○	○	◒	○	○	◒	◒	●	◒	◒	◒	◒	○	◒	○	○	○	○	○	○	○	○	○	○	◒	◒	◒
biomass specific growth rates	◒	◒	◒	◒	◒	◒	●	●	◒	◒	◒	◒	◒	◒	◒	○	○	○	◒	○	○	◒	○	○	◒	◒	◒
life cycle & reproduction	◒	◒	○	◒	◒	○	●	●	◒	●	◒	◒	◒	●	◒	●	◒	○	●	○	○	●	○	○	◒	◒	◒
intrinsic mortality	○	○	○	○	○	○	○	○	○	○	○	○	◒	○	○	◒	○	○	○	○	○	○	○	○	◒	◒	◒
predatory losses	◒	◒	○	◒	◒	○	●	◒	◒	◒	◒	○	◒	○	○	◒	○	○	◒	○	○	●	○	○	◒	◒	◒
temperature	○	○	○	○	○	○	●	●	◒	◒	◒	◒	◒	●	◒	◒	◒	○	●	○	○	●	○	○	◒	◒	◒
pH	○	○	○	○	○	○	○	○	○	○	◒	○	○	◒	○	○	○	○	○	○	○	○	●	○	◒	◒	◒
turbulence	◒	◒	○	◒	◒	○	◒	◒	◒	○	○	○	○	◒	○	○	○	○	○	○	○	○	○	○	◒	◒	◒

Figure legends:

Figure 1: Conceptual model of marine food web. P, phytoplankton; Z, zooplankton, N, nutrients, M, mixotroph, B, bacteria, D, detritus, HTL, higher trophic levels; solid arrows, inputs; dashed arrows, outputs; blue arrows; mixing; red and green arrows, exchange between the mixed surface layer and lower water.

Figure 2: Schematic of the inter-relationship between vital rates describing zooplankton growth. Almost all these features have equivalence in both protist microzooplankton and metazoan zooplankton; exceptions are indicated by *italic* script for microzooplankton. Colour coding indicates the parameter constants controlling these features of zooplankton physiology within classic NPZB models.

Figure 3: Dynamic risk assessment outputs from running the NPZB model (Fasham, 1993). Assessments were performed independently, utilising a Latin Hypercube routine applied to the feeding parameters (G_{max}; Panels A1 and A2 and K_{pred}; Panels B1 & B2 for phytoplankton and zooplankton respectively), assimilation efficiency of the zooplankton (parameter β; Panels C1 & C2 for phytoplankton and zooplankton respectively), nutrient regeneration (parameter ε; Panels D1 & D2 for phytoplankton and zooplankton respectively), and loss parameters (μ, Panels E1 & E2, and K_6, Panels F1 & F2 for phytoplankton and zooplankton respectively). For the assessment, the mean values of G_{max}, K_{pred}, β, ε, μ and K_6 were set as equivalent to the optimal value established by tuning the model to the data. Standard deviations for the assessment were set as 10% of the optimal value. Red line shows the mean outputs, with the green lines showing the 5% and 95% confidence limits.

Figure 4: Simulations of the grazing of the microzooplankton *Oxyrrhis marina* on the phytoplankters *Dunaliella primolecta*, *Isochrysis galbana* and *Micromonas pusilla*. Data (symbols) come from Fig. 5 in Flynn et al. (1996); model fits to data (lines) come from Fig. 5 in Mitra and Flynn (2006b). (A) Fits of the model using the prey selectivity function typically used in NPZ-type (e.g., Fasham et al., 1991) models. (B) Fits using the IS prey selectivity function proposed by Mitra and Flynn (2006b).

Figure 5: Respiration rates (gC $(gC)^{-1}$ d^{-1}) of microbial zooplankton of different cell size under starved conditions (open circle) and when presented with saturating food (closed circles); recreated by transformation of data in Fenchel (2005).

Figure 6: Examples of the different curve forms of the closure functions typically used.

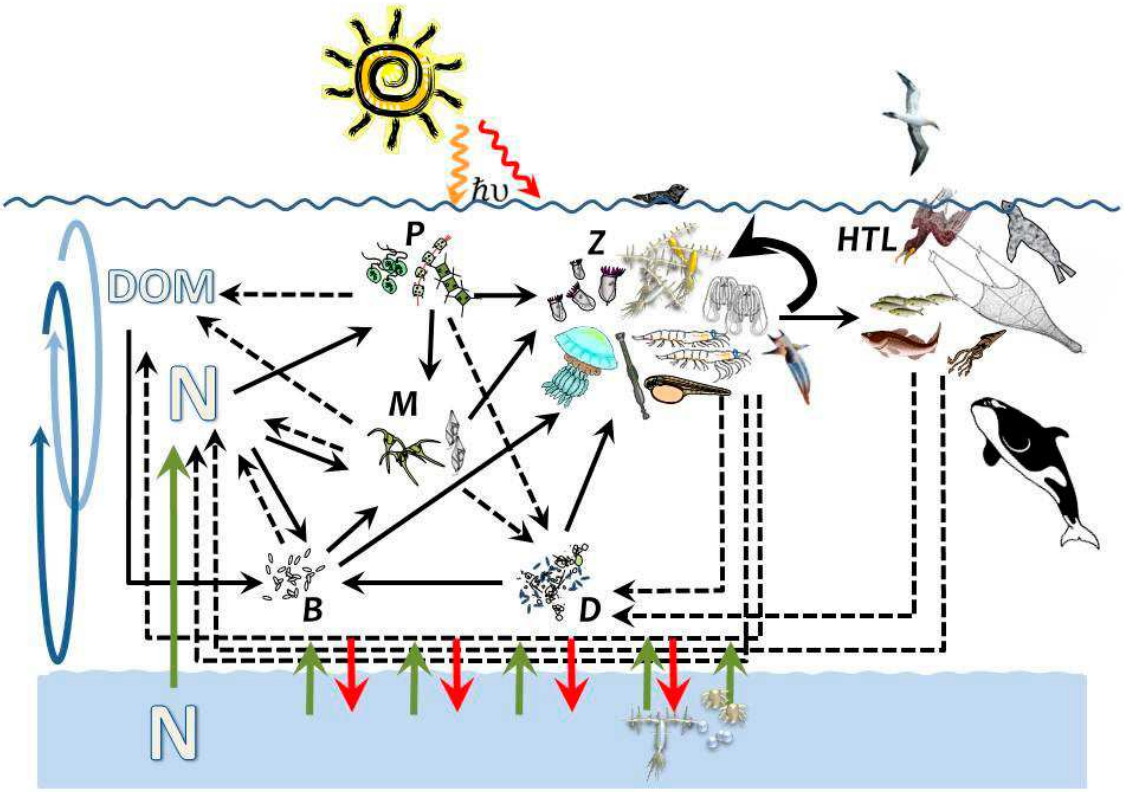


Figure 1

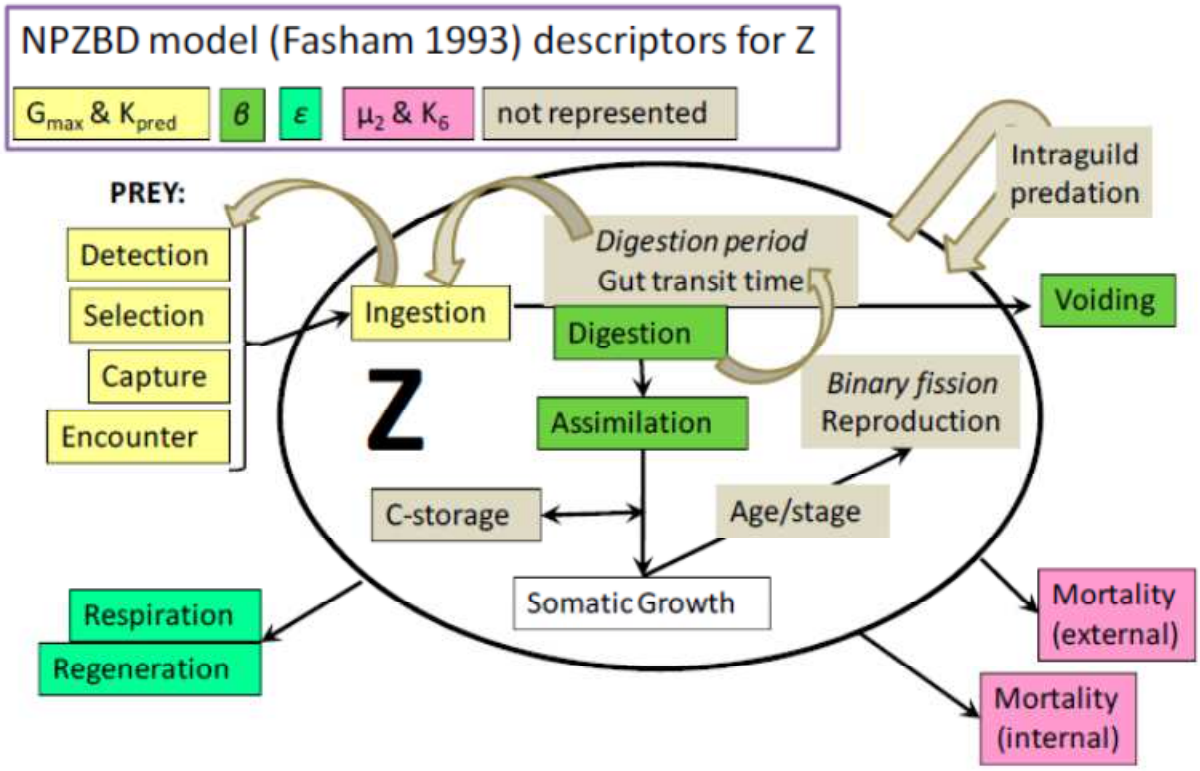
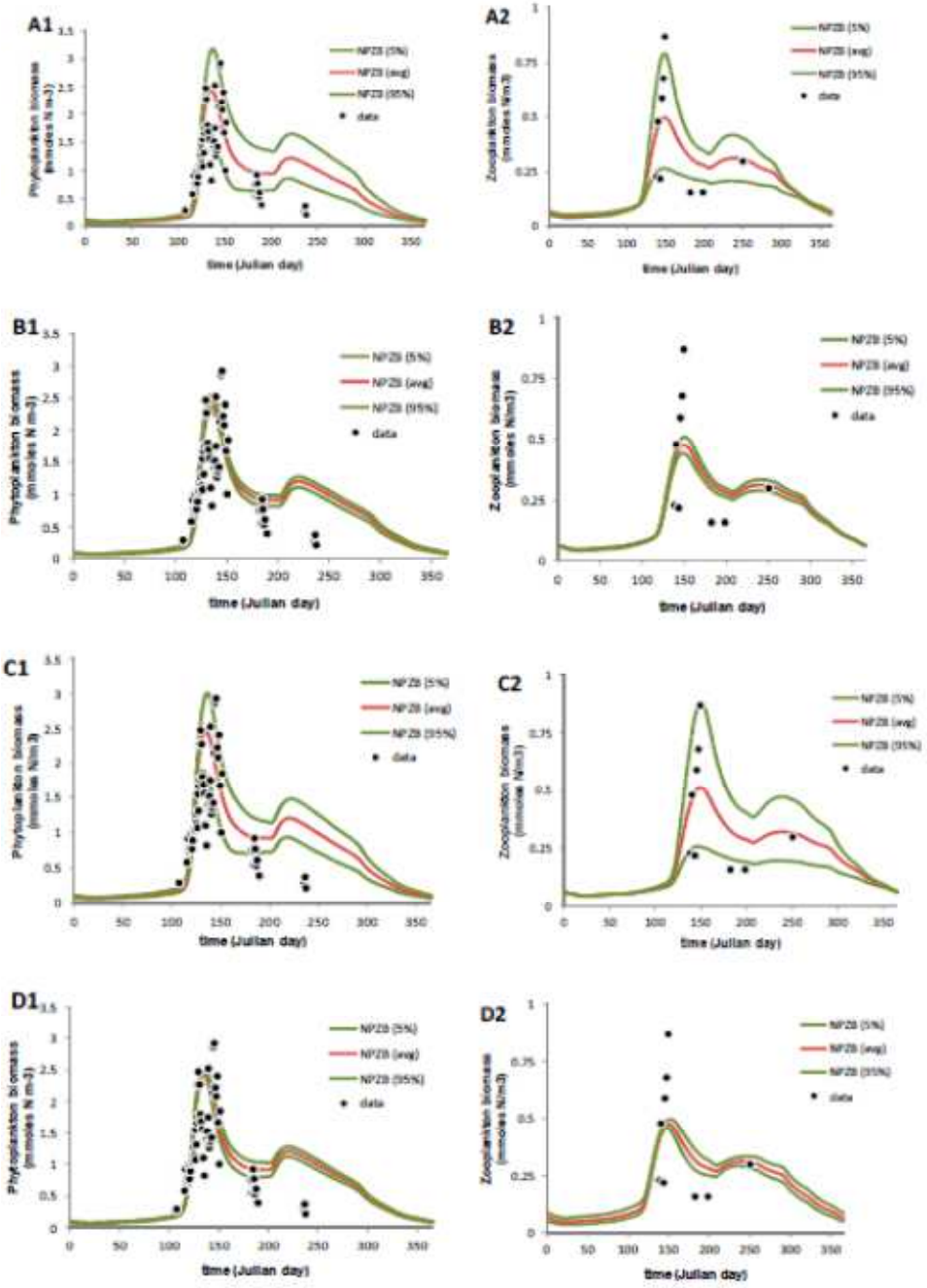

NPZBD model (Fasham 1993) descriptors for Z
G_{max} & K_{pred}
β
ε
μ_2 & K_6
not represented
PREY:
Detection
Selection
Capture
Encounter
Ingestion
Digestion period
Gut transit time
Digestion
Assimilation
Z
C-storage
Age/stage
Somatic Growth
Respiration
Regeneration
Intraguild predation
Voiding
Binary fission
Reproduction
Mortality (external)
Mortality (internal)

Figure 2

Figure 3


A1
A2
B1
B2
C1
C2
D1
D2
NPZD (5%)
NPZD (avg)
NPZD (95%)
data
time (Julian day)

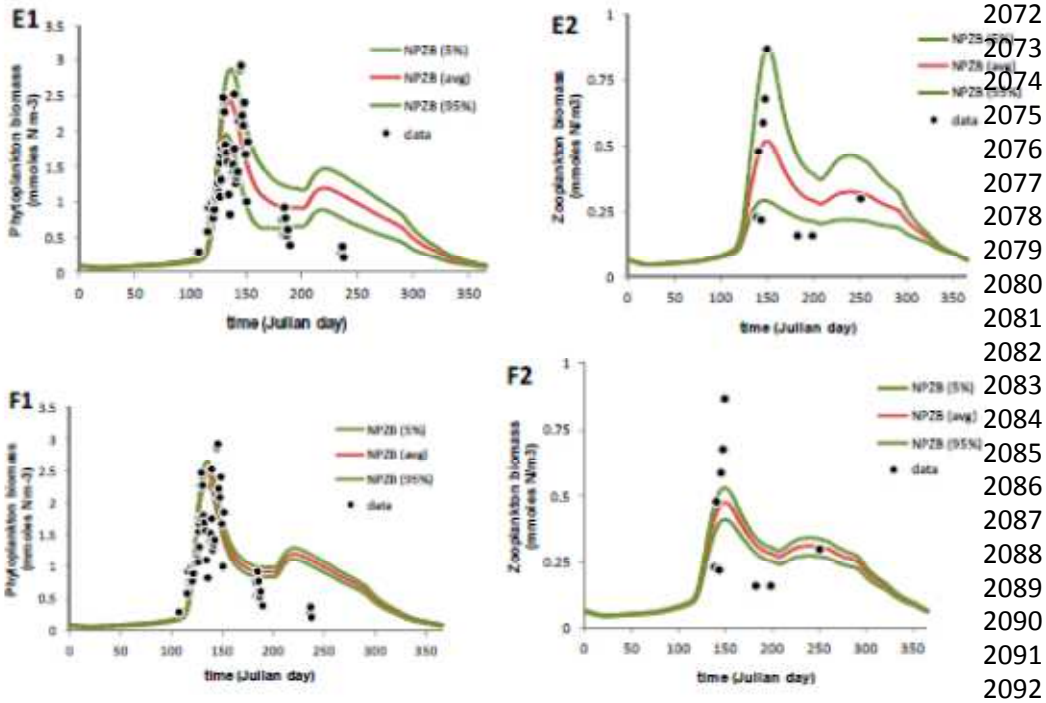
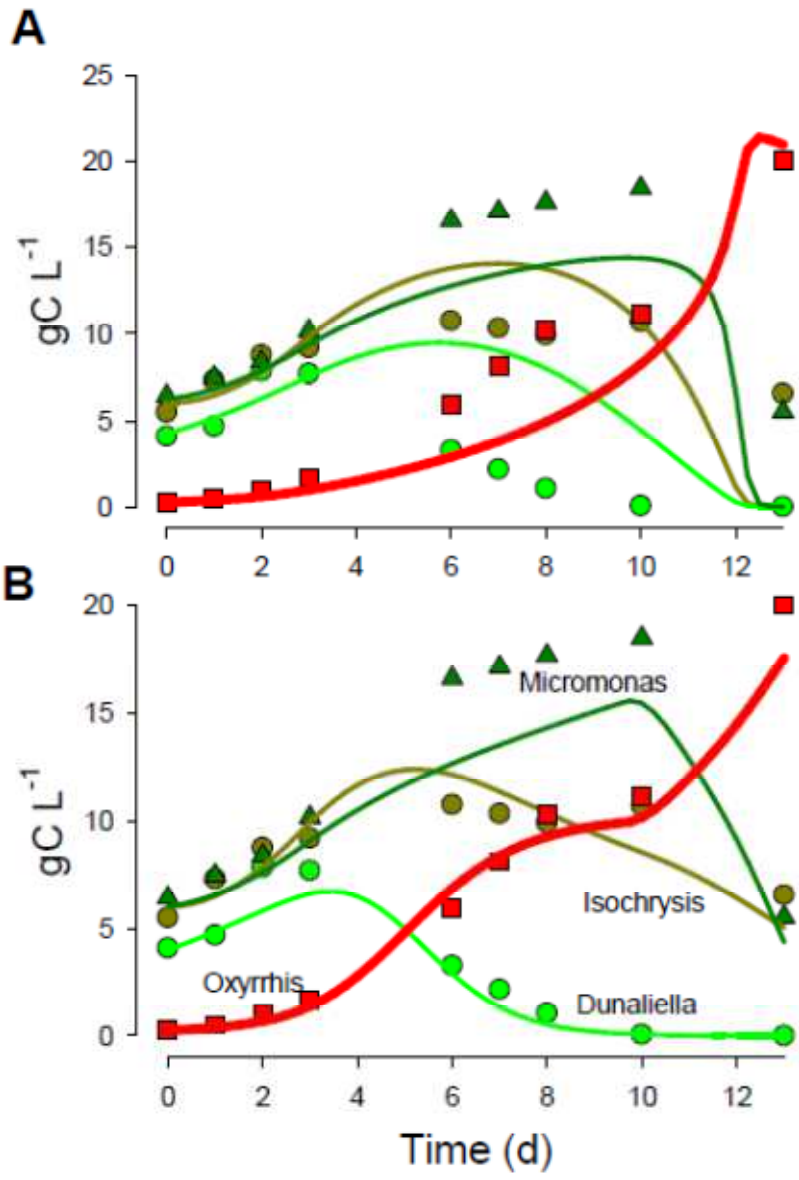


Figure 3 (cont.)

2106

2107



2108

2109

2110 Figure 4

2111

2112

2113

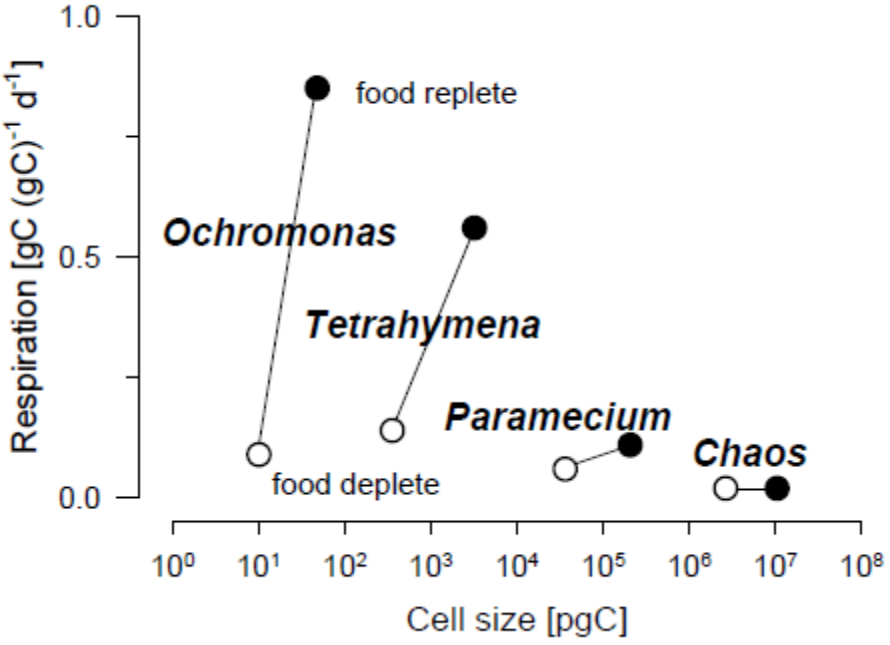

1.0
0.5
0.0
Respiration [gC (gC)$^{-1}$ d^{-1}]
food replete
Ochromonas
Tetrahymena
Paramecium
Chaos
food deplete
10^0 10^1 10^2 10^3 10^4 10^5 10^6 10^7 10^8
Cell size [pgC]

Figure 5

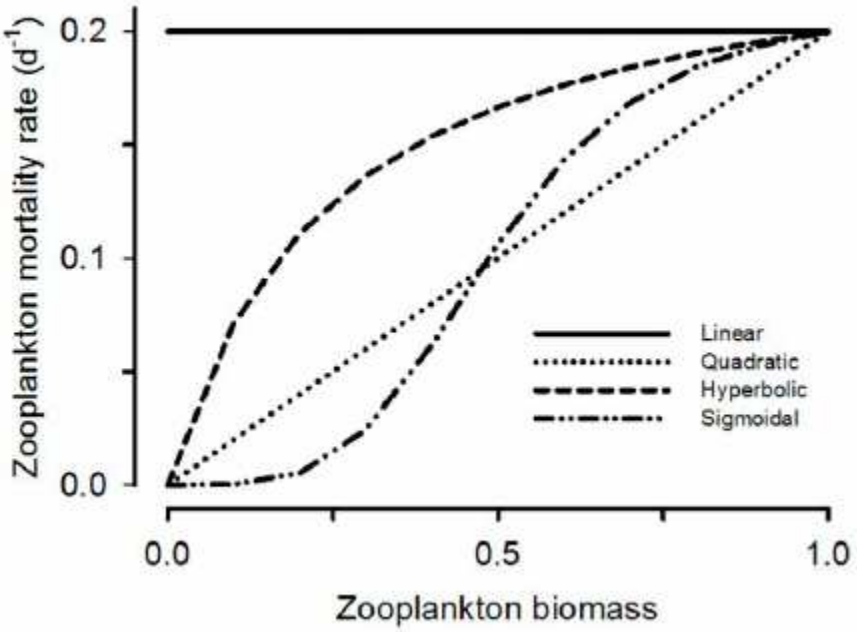

Zooplankton mortality rate (d^{-1})
0.2
0.1
0.0
0.0
0.5
1.0
Zooplankton biomass
Linear
Quadratic
Hyperbolic
Sigmoidal

Figure 6